ELEMENTS

OF

PHYSIOLOGY,

FOR THE USE OF STUDENTS,

AND WITH PARTICULAR REFERENCE

TO THE WANTS OF PRACTITIONERS.

BY

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TRANSLATED FROM THE GERMAN, WITH ADDITIONS,

BY

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PREFACE.

There is no want, in the present day, of excellent elementary works on Physiology; but with the late rapid and incessant growth of this science, it seems to the Writer that several such works, each conceived in its own spirit, may advantageously exist side by side, he has therefore resolved to publish an Elementary Treatise on Physiology himself.

The great object which he proposes in this undertaking, and to which he will hold all others subordinate, is this: To give the most concise and clear view possible of the older and newer Physiological Inquiries in a systematic form, and with particular reference to Practical Medicine.

The work is divided into four Parts.

The *First* embraces the subjects of GENERATION and DEVELOPMENT.

The *Second* comprises the subject of NUTRITION;

The *Third* treats of SENSATION and MOTION;

The *Fourth* Part will include the GENERAL PHYSIOLOGY.

The reasons for this arrangement the Writer imagines must be apparent in its announcement. The General only becomes intelligible when the Particular has been analytically investigated; it is only after the consideration of the several special vital processes, that secure advances can be made in their contemplation in the aggregate and as they are associated. On this account is the General Physiology postponed till the Special Physiology has been discussed.

The Physiology of Man is to be understood as the peculiar object of the work; every unnecessary deviation into the domains of Comparative Anatomy and Physiology has

therefore been avoided; with this, however, a comprehensive glance has been taken, not only over the animal, but even over the vegetable world, whenever comparative views seemed requisite to the right understanding of processes in their last complexity, or where an appeal to lower organisms became indispensable to the elucidation of physiological facts in higher grades of creation.

As supplementary to the present undertaking, and with a view to the comprehension of the morphological substratum of physiology, the Writer determined to produce at the same time an Atlas of Plates, under the title of ICONES PHYSIOLOGICÆ. Like the Work itself, the Atlas has appeared in three fasciculi, having reference to the three grand divisions of Special Physiology. The Elements of Physiology and this Atlas may therefore be understood as having a mutual reference to one another, but each is nevertheless complete in itself.

In writing the Elements of Physiology, the Author has had his eye particularly upon the STUDENT and the PRACTITIONER of MEDICINE; but he has not been unmindful of any one who would obtain a comprehensive view of the recent progress and present state of physiology. He has striven especially to make his book a guide in the path of observation and experiment to those who, remote from the appliances of great cities and amply-furnished institutions, are still anxious to investigate and to prove for themselves, with such means as they have at their command. Even to the physiologist of higher pretensions, however, he would fain hope that he had presented a work not unacceptable on many accounts; for it has still been his endeavour to see where it was possible with his own eyes, and to speak at all times as feeling himself firm on his own footing. With all this he cannot but hold himself doubly secure in the support of the distinguished physiologists who have furnished him original contributions upon those

subjects to which they have more particularly devoted their attention. In the First Part he has to acknowledge valuable observations from his friends, BISCHOFF, SCHWANN, VALENTIN, and E. H. WEBER, and in the Second Part, from Dr. JULIUS VOGEL, which will be found engrafted in their proper places among the annotations, or in the body of the text.

RUDOLPH WAGNER.

GOTTINGEN, 1842.

NOTICE BY THE TRANSLATOR.

THE foregoing advertisement of the Author leaves little to be said by his Translator: but if in a country like Germany, where there is already no want of even excellent elementary treatises on Physiology, it was believed that another might advantageously see the light, surely in England, where there is something like a dearth of works of this kind, especially of native growth, ample room must be found for the transplantation of one of moderate pretensions, indeed, but of unquestionably high character.

Engaged, of late years, in delivering Lectures on the Theory and Practice of Medicine, and forced in the discharge of this task upon a more than usually close meditation of the great Principles of the Healing Art, as flowing immediately from a knowledge of the Laws of Life, the Writer felt peculiar pleasure in meeting with the Elements of Physiology of Professor Wagner; here he seemed to find embodied all that he was in search of in a System of Physiology; the practical character, it struck him, was never more obviously stamped on any production of mind than on this, and seeing that the work was all it purported to be, "A concise and clear Statement of the Doctrines of Physiology in a systematic form, and bearing particularly upon Practical Medicine," he thought that he would be held as conferring

a boon upon the medical and, perchance, even on the general literature of Great Britain, did he present the work in an English dress; for Physiology, indispensable to the practitioner of medicine, is also the first and most essential element in the general science of man.

The anatomical basis upon which Special Physiology in the present day so entirely rests, made it almost imperative on the Translator to adopt the ICONES PHYSIOLOGICÆ of the Author as an element in the work. This has accordingly been done to a very great extent; and carefully engraved in wood by our excellent artist, Mr. Vasey, and incorporated with the text in their proper places, the Writer trusts that these valuable means of Illustration will be deemed to have been used in the most advantageous manner.

With regard to *additions*, the Writer saw that one great merit of Dr. Wagner's work was its conciseness. He has been chary in lessening its claims to the attention of the Student and Practitioner, by taking away from this most rare and excellent quality. In consideration of the daily, the hourly, advances of Physiology, however, he believed that besides sweetening his labour, he could make the work more thoroughly English by appending a few annotations both on his own motion, and on the hint of more than one excellent Anatomist and Physiologist. To his kind friend Mr. George Gulliver in particular, he is indebted for several original observations, and for numerous suggestions in the course of his agreeable labour. The few additions which have thus been made, the Writer would fain hope will be found to place the work fairly on a level with the state of knowledge on the various departments of the Special Physiology at the present hour.

R. WILLIS.

LONDON, 1844.

FIRST DIVISION:

THE

SPECIAL HISTORY OF THE VITAL PROCESSES.

BOOK THE FIRST:

OF GENERATION AND DEVELOPMENT.

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[MICROMETRIC MEASUREMENTS.

The Standard for micrometric measurements very generally followed in Germany, and adopted in this work, is the fraction of a Paris line. In Great Britain, minute objects are usually measured in fractions of an English inch. The Paris inch contains twelve lines, and is longer than the English inch, in the proportion of 1.06575 to 1.00000; that is, the Paris inch is equal to 1 and $\frac{1}{15}$th of an inch English very nearly. Assuming this ratio to be sufficiently correct for all practical purposes, it is easy to convert fractions of a French line into fractions of an English inch, by multiplying the denominator of the former by the number 11.25. R. W.]

ELEMENTS OF PHYSIOLOGY.

BOOK THE FIRST.

OF GENERATION AND DEVELOPMENT.

SECTION THE FIRST.

OF GENERATION.

THE SUBJECT AND MODE OF TREATMENT.

§ 1. In the act of GENERATION two different matters or elements are brought to exert an influence upon each other. These elements are formed and separated from the blood in the germ-preparing organs of the male and female, when they have attained their maturity. The male generative element is called SEMEN (SPERMA), *seed;* the female, OVUM, *egg.* As the effect of an intimate conjunction of both of these elements, the EMBRYO is evolved, which proceeds to its ulterior development either within or without the body of the mother. The act of generation is complete, when the maternal generative element has been consumed or exhausted, and the various organs of the embryo are so far developed, that it is fitted to assume an independent existence, and to take nourishment from without. The DEVELOPMENT OF THE EMBRYO would consequently appear to be but a second stage or division of the generative act.

§ 2. In our exposition of the elements which enter into the generative act, we shall follow at once an analytic and a synthetic method. We shall begin with an analysis of the germ-preparing organs and generative matter in the male, next investigate the primary formations in the germ-preparing organs of the female, and

wind up these anatomico-physiological notices with a general account of the forms of the sexual system, in the course of which the usual amount of knowledge of human anatomy will be presumed. We shall then proceed to consider the phenomena that accompany the encounter of the two matters essential to generation, particularly describing the general occurrences of the first moment of the generative act, which afford an explanation of some questions connected with the subject[1].

CHAPTER I.

ANALYSIS OF THE GERM-PREPARING SEXUAL ORGANS, AND THEIR PRODUCTS.—MICROSCOPIC ANALYSIS OF THE SPERMATIC FLUID.

§ 3. THE SPERMATIC FLUID (*sperma, semen*), which is secreted in the testicles of all male animals capable of reproduction, is of thick consistency and a whitish colour. This fluid is obtained for analysis in greatest purity, and most completely formed, when a drop of it is taken directly from the epididymis or vas deferens and transferred to the field of the microscope. Care must be taken to choose the

[1] The majority of the older works on generation have, at the present day, merely an historical value. They mostly consist of pure speculations, without any foundation in fact or observation: these works will be referred to by-and-by in our History of Physiology, and also in the different sections of the present book. The most remarkable among the older works is, undoubtedly, that of Harvey, *Exercitationes de Generatione Animalium*, Lond. 1651, in 4to. The writings of *Regner de Graaf*, entitled, *De Virorum Organis generationi inservientibus*, Lugd. Batav. 1668, in 8vo, and *De Mulierum Organis*, &c. ib. 1672, are also of great importance. Copious summaries of all the observations of the older writers may be found in Haller's *Elementa Physiologiæ*, vol. vii. p. 410. 1765. Among the writings of more recent date which treat of the subject of generation generally, we must particularly refer to that of Spallanzani, *Expériences sur la Génération par Senebier*, Genève, 1783, translated into German, by Michaelis, Leipz. 1786; [and into the English, in *Tracts on the Natural History of Animals and Vegetables*, by Dalycll, Edin. 1803;] to that of Oken, *die Zeugung*, Bamberg and Würzburg, 1805; of Prevost and Dumas, *Nouvelle Théorie de la Génération*, *Annales des Sciences Nat.* tom. i. ii. and vi.; of Burdach, *Physiologie*, B. i. (second edition,) 1835, which contains a very copious account, but is not complete as regards the numerous recent observations. The best and most comprehensive view of the whole subject of generation, grounded on personal observation, which we possess, is that by Dr. Allen Thomson, in his article, Generation, in *Todd's Cyclopædia of Anatomy and Physiology*, vol. ii. The writings of Wolff, Blumenbach, and others will be particularly quoted by and by.

body of an animal just killed, or a perfectly recent human subject, that the semen may be studied before it has undergone any change. A small quantity of albumen, or of the serum of the blood, has no effect in altering the semen, and affords the best means of diluting and spreading sufficiently the globule of spermatic fluid destined for examination. Properly reduced and extended, the fluid is then to be covered in the usual way with a thin plate of glass (or mica [2]). Under a magnifying power of three or four hundred diameters, there is immediately brought into view a multitude of minute bodies, closely crowded together even in the attenuated fluid, and among which, when the semen is that of an animal but lately dead, a more or less active motion prevails. These moving bodies, ever since their discovery, have been spoken of under the name of the *seminal animalcules*, or *spermatozoa* [3]. At first sight, if un-

[2] Albumen, or, still better, serum of the blood, is the best thing for diluting organic fluids, or covering the surface of tissues, which we would analyse with the microscope. Pure water generally produces some change; but water with from one-tenth to one-twentieth of sugar or common salt dissolved in it, may in many cases be substituted for the fluids above mentioned. A little practice enables us to determine the proper degree of dilution, &c. Blood-serum is, perhaps, most quickly and conveniently obtained from frogs, which it is now the custom with all who give any attention to physiology, to keep by them alive through the whole year. The heart of one of these animals is opened, and the blood allowed to flow into a test-glass of narrow diameter, where it is beaten or stirred with a glass rod; after a time, the globules begin to separate, and by-and-by fall to the bottom, the serum swimming above them. This fluid will keep for a considerable number of days even in summer; in winter, of course, it remains unchanged much longer. Pieces of glass are conveniently used in many cases for covering objects for the microscope, where they do not suffer from pressure. The seminal animalcules are so small and delicate, that their motions do not appear to be impeded in the slightest degree by the pressure of one plate of glass upon another.

[3] The discovery of the seminal animalcules is cotemporaneous with the invention of the microscope. A student from Leyden, named Ham, appears to have been the first (August, 1677,) who observed them. He shewed them to Leeuwenhoeck, who followed up the discovery as an object of science, and communicated the results of his observations to the Royal Society of London. Leeuwenhoeck's excellent observations and figures are contained in the collection of his works, entitled *Opera Omnia s. Arcana Naturæ*, 4to. Lugd. Batav. 1722; and, in the *Arcana Naturæ detecta*, ibid. 1722, (published as a second volume to the foregoing work). Later and very useful observations are contained in Von Gleichen's *Treatise on Seminal and infusory Animalcules*, (*Abhandlung über die Samen- und Infusionsthierchen oder über die Erzeugung, &c.* Nürnberg. 1778), 4to. The publication of the numerous observations and figures of Messrs. Prevost and Dumas (in various volumes of the *Annales des Sciences Naturelles*), may be said to mark a new epoch in this subject. Czermak's Contributions to

diluted semen have been used, the entire fluid appears to consist of these animalcules. With more careful examination, however, other minute, round, granulated bodies may almost always be detected. At one time these are seen singly, and few in number; in others they are more abundant; in every case, however, they are much less numerous than the spermatozoa. These bodies may be distinguished by the name of *seminal granules, granula seminis*. Both elements of the semen are suspended in a small quantity of perfectly homogeneous fluid, transparent and as clear as water. This *liquor seminis* is most distinctly seen around the edges of a drop of undiluted spermatic fluid brought into the field of the miscroscope. Frequently, or indeed commonly, the liquor seminis is present in such small quantities, that it is discovered with the utmost difficulty. It may, however, be frequently rendered more obvious by the use of some reagent, such as acetic acid or alcohol, by which the fluid, albuminous apparently in its nature, is coagulated, and then appears as an exceedingly delicate granular matter, intermixed with the spermatozoa and seminal granules. Pure semen, therefore, in its most perfect state, consists principally of *seminal animalcules* and *seminal granules*, both of which are enveloped in a small quantity of fluid, which I name *liquor seminis*.

§ 4. The LIQUOR SEMINIS, from its transparency and homogeneousness, cannot be made the subject of any more particular microscopical inquiry. We possess no means of isolating it, and investigating its nature apart from the other elements of the spermatic fluid, as we do in regard to so many of the other animal

the history of Spermatozoa (*Beiträge zu der Lehre der Spermatozoen*, Wien, 1833), is, as its title implies, especially devoted to the Spermatozoa; the more delicate details in regard to outline are overlooked in the figures attached to this treatise, apparently from the use of too high a power, and an instrument deficient in definition. I myself gave a short critical notice of antecedent labours, and added many new representations of the seminal animalcules, particularly of the vertebrata, in my *Fragments on the Physiology of Generation*, and *Contributions to the History of Development*, which are contained in the second volume of the Transactions of the Royal Academy of Sciences of Bavaria, for the year 1837. (*Abhandlung der Mathem. Phys. Klasse der Königl. Bair. Akad. der Wissenschaft.*) Siebold, of Dantzig, has given excellent and very accurate observations on the spermatozoa of the invertebrata especially, in Müller's *Archiv für Physiologie*, (1836, S. 13, und 232; 1837, S. 381). I would also refer to the copious critical extracts from Siebold's and my observations in Valentin's *Repertorium*, Bd. 2, S. 133 (1837). The opinions and knowledge in regard to the seminal animalcules of the older writers will be found displayed in a very complete manner in Ehrenberg's recent great work on the *Infusoria* (*über die Infusionsthierchen*, S 465.)

fluids,—the blood for instance. In animals, with blood-globules of considerable size, such as frogs, it is easy to separate the liquor sanguinis from the solid elements by simple filtration; the serum passes through, the globules remain upon the filter. But the filter stands us in no stead in regard to the spermatozoa; these are too minute to be stopped by the meshes of any filter we can use; they pass through with the liquor seminis; and then, the thick and tenacious semen adheres so intimately to the surface of a filter, that frequently nothing whatever will pass. If a quantity of spermatic fluid be left standing for several hours or days in a test-glass, still the liquor seminis does not separate, or at most it appears as a thin line around the edge of the fluid[4].

The SEMINAL GRANULES resemble the granules of the lymph. They are colourless bodies, that yet present pretty dark outlines, round, or perhaps somewhat flattened in shape, having, as it seems, a finely granular surface, and measuring in general from the $\frac{1}{300}$th to the $\frac{1}{500}$th of a line in diameter, (fig. I. *a e*, and particularly fig. VI. A, *c*, and fig. VII. *b*). Whether they have a nucleus or not, has not yet been certainly ascertained[5]. Besides

[4] It is most easy to obtain conviction of the existence of the liquor seminis in the manner already mentioned (§ 3), namely, by the addition of a drop of acetic acid or of alcohol to the undiluted spermatic fluid; besides the alteration produced in the spermatozoa by this addition, quantities of fine granular bodies make their appearance. Occasionally the spermatozoa are in such numbers, and the liquor in question in such small quantity, that I have failed to make it manifest in the manner indicated; repeated failures ought not, therefore, to lead to any erroneous conclusion in regard to this matter. The greater number of my experiments were made upon frogs and rabbits, and it was in them that I could most completely satisfy myself of the existence of the liquor seminis. Sometimes, besides the minutely granular bodies, irregular coagula, similar in all respects to those that are produced in albuminous fluids on the addition of re-agents, make their appearance; this is usually more particularly the case about the edges of the drop, where fewer spermatozoa are congregated. The experiment is best made with alcohol; with acetic acid, the cloudiness and minutely granular precipitate are occasioned less certainly or less perfectly; if a mixture of alcohol and acetic acid be used, small coagula are immediately produced.

[5] The seminal granules, *granula seminis*, appear to be regularly constituted, and genuine elements of the spermatic fluid, and by no means altered epithelial cells or nuclei; these last are easily distinguished, mingled with the semen at the same time, and are always to be met with, in consequence of the process of desquamation that is continually going on from the epithelium. They are always paler in colour, more flattened, and have never such dark margins as the proper seminal granules. It must be allowed, nevertheless, that it has hitherto been impossible to say, with certainty, whether these granules are plastic seminal elements,—products of the proper secreting function of the testis, or mere products of the epithelium cells. I have found them in the seminal fluid of man

these corpuscles, others of a different nature are occasionally, but not invariably met with in the semen of the higher vertebrata. These are minute shining globules, having dark edges, refracting the light powerfully, and bearing the strongest resemblance to small fat or oil-globules[6], (fig. VI. B, *a* and *b*, from the testis, p. 26). Occasionally, too, we find molecules of still smaller dimensions, which exhibit the Brownian molecular motion; it is still doubtful whether these are proper and especial corpuscles, or—and this is more probable—detached portions of the other co-existent larger bodies.

As accidental, yet very general and abundant elements of the spermatic fluid must be reckoned the detached epithelium cells, which we must be careful not to confound with the proper seminal granules. Sometimes considerable shreds of epithelium, with the cells tessellated, are observed.

§ 5. The SEMINAL ANIMALCULES or SPERMATOZOA, by reason of their singular variety of forms, their vital peculiarities and mode of development, are, of all the elements of the spermatic fluid, those which naturally attract the attention of the observer first

and all animals, sometimes very scantily mingled, at other times in great quantities—a fact easily verified, by examining the semen of birds of the same species, of the chaffinch, *fringilla cœlebs*, for example, at different times. It has very certainly appeared to me, however, that in regard to quantity, the granula seminis stand in direct proportion to the energy of the seminal secretion; they are thus infinitely more abundant in birds at the period of the greatest turgescence of the testis, and repletion of the vas deferens, than at any other season. The dimensions of these granules vary considerably in the same animal. The measurements given above are the mean; but granules also occur commonly enough of the $\frac{1}{200}$th, the $\frac{1}{150}$th, more rarely of the $\frac{1}{100}$th of a line in diameter, and down to $\frac{1}{500}$th and $\frac{1}{600}$th of a line.

[6] The bodies mentioned as bearing so strong a resemblance to oil or fat-globules, I have occasionally met with in the fully formed spermatic fluid of the vas deferens of animals of every class. They occur more rarely in man, and in him much more sparingly in the semen of the vas deferens than in that of the tubuli of the testis itself. The globules vary in their dimensions, but, in general, they are smaller, less definite in their outline, never granulated or punctuated on their surface (so that they are not aggregates of any finer molecules), and, with a little practice in the use of the microscope, readily to be distinguished from the granula seminis. Globules of the kind now under consideration, and of the $\frac{1}{800}$th of a line in diameter, I have repeatedly, but not invariably detected in the seminal fluid of the hedgehog, for example, of the bat and other animals. Now and then these very minute globules were observed to flit rapidly across the field, in virtue of a faculty of motion apparently inherent in themselves, of a power certainly not referable to simple molecular motion. Are they monads? ova of the spermatozoa?

and most powerfully. They exist in the semen of all animals capable of procreation[7]; in plants, also, some insist upon having discovered elements of the same description[8]. The animalcules

[7] Men and animals are capable of procreating only at or within certain ages. In these latitudes the period of PUBERTY, when the capacity of engendering is first developed, arrives generally between the fifteenth and eighteenth year in the male, and is proclaimed by involuntary nocturnal discharges of the spermatic fluid; in the female the age of puberty is usually attained between the thirteenth and fifteenth years; now and then it is reached as early as the twelfth year, and sometimes even sooner. The period of sexual maturity in the female is proclaimed by the appearance of the catamenia, or menses (*menstruation*); every four weeks, according to the rule, a discharge of blood takes place from the uterus; this discharge lasts for several,—three, four, or five days, and is accompanied by the detachment or exfoliation of the delicate epithelium of the mucous surface of the uterus, which is again and speedily reproduced. The excreted blood is little disposed to coagulate, and generally of a dark colour. Among animals a similar phenomenon has been observed only in monkeys and bats. In man and the domestic animals, birds as well as mammalia, the germ-preparing sexual organs are usually at all times active, and reproduction may take place at every season; among wild animals, on the contrary, the reproductive faculty is limited to a certain short period of the year; the time during which the sexual inclination prevails among animals is called the *heat*, the *rut*, &c. It mostly occurs early in the spring, sometimes in the autumn. It is during this period only that the testes and sexual organs are turgid, and that seminal animalcules are abundantly and regularly produced. In the human female the capacity of reproducing is generally lost between the forty-fifth and fiftieth years; in the male the reproductive energy declines only as he advances in years; healthy men seem capable of engendering to the very end of their lives, and examples are not wanting of men in their seventieth, eightieth, and even their hundredth year, and more, becoming fathers. Thomas Parr, in his hundred and forty-second year, showed himself still capable of fruitful sexual intercourse. I have constantly found semina animalcules in the fluid of the testis of very aged men; it is only among weakly and decrepid individuals that the procreative faculty is really lost.

[8] With regard to the so-styled animalcules of the pollen-fluid of plants, opinions even among the latest and best observers are very much divided. The pollen and the pollen-capsule contain a somewhat tenacious fluid, in which minute bodies are suspended; this matter of the pollen-globule has been regarded as the vegetable seminal fluid—*Fovilla;* Adolphe Brongniart compared its suspended molecules to the seminal animalcules, and even observed the bendings that take place in them in the Hibiscuses and Œnotheras (vide his *Rech. sur la Génération*, &c. in *Ann. des Sc. Nat.* XII. p. 34. 1827). Similar observations have been made by Mr. Brown, On the particles contained in the pollen of plants, &c. Lond. 1827, and in *Vermischte Schriften*, Bd. IV. S. 146). Others, again, Hugo Mohl, &c. have denied all change of form in these molecules, and regard them as mere starch-granules (vide Mohl's *Beiträge zur Anat. u. Physiol. der Gewächse*, I. S. 32). Mohl found the smallest granule of the Fovilla which he could measure to be the $\frac{1}{10000}$th, and the largest the $\frac{1}{100}$th of a Paris line in diameter. Many observers reduce all appearances of motion in these granules to mere molecular movement. Meyen, on the other

must be examined, as obtained from the epididymis, or vas deferens, if we would observe them possessed of their most perfect form, size, and vital endowments. The first circumstance that strikes the observer in regard to these animalcules, is their diversity of form in the different classes, genera, and species of animals. In Man (fig. 1, *a*—*d*), they are extremely small, scarcely sur-

hand, maintains that the seminal animalcules are particularly obvious in the Œnotheras; and, again, Schleiden (in Wiegmann's *Archiv*, 1838, S. 56) proclaims all the spermatozoa of plants to be mere starch-grains. Fritsche, in his very excellent observations on Pollen (*Beob. über den Pollen*, Petersburg, 1837), expresses the same opinion. The elements of plants that bear the closest resemblance to the spermatozoa of animals, are those granules with tails which are found in the capsules of the mosses, and which, as obtained from the genus *Sphagnum*, were already subjects of observation among the older inquirers. Unger and Werneck have given a particular account, and published figures of these bodies, and regard them as true spermatozoa (*Regensb. Botan. Zeitung*, 1834, S. 145). Meyen has very recently described minutely the caudate spermatozoa of the anthers of *Marchantia polymorpha* (Wiegem. *Archiv*, 1838, S. 212). Valentin holds the bodies in the Fovilla of vegetables to be merely Brownian molecules; he has not observed the animalcules of Sphagnum and Marchantia; the grand criterion of true spermatozoa, viz. internal organization and development in cysts, has never been asserted in regard to the so-styled spermatozoa of plants (Valentin's *Repertorium*, 1838, S. 63). I have not myself, I regret to say, had any opportunity of making observations on Sphagnum, having for several years sought in vain for anthers in specimens of this genus procured from the most opposite habitats. In other mosses, however, Orthotrichum, Fumaria, &c. I have never discovered any caudate corpuscles, and the contents of the anthers appeared to me to be affected only by the universal molecular motions, which proceeded amidst tincture of iodine as before. In the

Fig. I.

Fig. I.—Spermatozoa (magnified from nine hundred to one thousand diameters) taken from the vas deferens of a man shortly after death; *a*, spermatozoon presenting the flat surface; *b*, ditto, viewed in profile, the margin being presented; *c*, ditto, presenting the circular spot on the surface, which some suppose to be a sucker; *d*, a spermatozoon exhibiting a process from the anterior extremity of its body, not unlike a proboscis; *e*, seminal granules.

passing the $\frac{1}{50}$th, and, at the very most, the $\frac{1}{40}$th of a line in length. The little, oval, somewhat flattened, almond-shaped, and perfectly transparent body, seldom exceeds from the $\frac{1}{600}$th to the $\frac{1}{800}$th of a line in length; the filiform tail at the top is thickish, and so strong, that the double contours are plainly visible; but, towards the end, it becomes so fine, that it cannot be followed even with the highest powers to the point; so that it is possible the delicate extremity proceeds farther than it can be traced, and that the animalcule is actually longer than it can be determined to be by micrometic admeasurement[9]. In the Mammalia, the spermatozoa

anthers of Marchantia polymorpha, however, besides the minute black globules, I observed several green corpuscles, the rapid motions of which seemed to indicate the existence of a tail; this was also made completely manifest by the addition of tincture of iodine, which arrested the motions. These green corpuscles are decidedly smaller than human spermatozoa. I have not observed with equal precision the peculiar larger, elongated, yellowish, transparent corpuscles of the Fovilla of Œnothera biennis and other species; the motions of these, however, I may say, appear to me to be of a voluntary or spontaneous kind. The length of these corpuscles varied between the $\frac{1}{600}$th and the $\frac{1}{800}$th of a line; in tincture of iodine they became quiescent and opaque, and resembled aniseeds in shape; the motions of the smaller molecules continued after the addition of the iodine. (See farther on this subject the observations under annotation 69, to § 22.) On the older researches of Brongniart and others, see the Summary in Von Roeper's translation of De Candolle's *Physiologie Vegetale,—die Pflanzen-physiologie*, &c. Bd. II. S. 103. Meyen proposes to treat the entire subject in the third volume of his *Pflanzen-physiologie*.

[9] Dujardin (*Ann. des Sciences Nat.* VIII. p. 293, and pl. 9, 1837) describes and figures certain irregular knots and lobular enlargements at the root of the tail of human spermatozoa. These appearances I have myself observed, but they only occur as effects of certain alterations undergone by the animalcules, in consequence, for example, of their long stay in urine, especially when this fluid contained at the same time a quantity of puriform sediment. I have always found the size of the bodies of the spermatozoa to be very nearly the same in the same individual. But on the other hand I have noted them of such dissimilar magnitudes in different individuals, that I was led to regard this as more than accidental, and as a consequence of changes undergone either from the different periods that had elapsed since the death of the individual, or from the influence of the fluids, the urine for instance, with which they had been in contact. I therefore instituted a series of inquiries on the bodies of suicides, in as fresh a state as possible, and mostly of strong men. In one man of twenty years of age, and in another of fifty (both of whom had put an end to their lives by hanging), I found the bodies of the seminal animalcules exceedingly small and roundish, the $\frac{1}{800}$th of a line and under in length; in a third individual, in his fortieth year, who had also hanged himself, I, on the contrary, observed the animalcules all of very large size, the bodies being about the $\frac{1}{500}$th of a line in length. The whole of them were very nearly of the same size, and greatly resembled one another. Farther observations on this point would be interesting. Occasionally the seminal animal-

present very similar forms (fig. III. 1—9); but they are generally larger than in man, and this more especially among the smallest animals: in the genus Mus they are perhaps larger than in any other family; in the rat, for example (fig. III. 7.), they are of the $\frac{1}{12}$th of a line, and perhaps more, in length; the body measures from the $\frac{1}{150}$th to the $\frac{1}{200}$th of a line; the tail is here thick and strong, and easily traced to its extremity. The forms of the body, or anterior thicker end of the spermatozoa, are manifold: in apes (fig. III. 1) these animalcules resemble those of the human subject; they are only somewhat larger: in the mole (fig. III. 3) they are longer; they are more pyriform, but also greatly flattened and very various, both in figure and size, in the dog (fig. III. 4), in the rabbit (fig. III. 5), in the roebuck (fig. III. 9), and still more in the genus Mus:—in the rat (fig. III. 7) the body posteriorly is sickle-shaped, arched, and extremely compressed, but long; the tail springs more from the upper and back part of the body; a great general resemblance to this last form is apparent in the spermatozoon of the common mouse (fig. III. 6), only the body is shorter; the point above, merely indicated and scarcely bent, resembles, when viewed from the side, a round-edged scalpel (*a*); the body is deepened posteriorly where the root of the tail is set on (*b*); these particulars are still more strongly seen in the field-mouse (fig. III. 8, *b*), the body

cules exhibit a yellowish, even an amber, tint. Perhaps this is a mere effect of refraction. As a remarkable departure from the normal form, I have upon two occasions observed the caudal end of the body double, bifid, or forked; I do not imagine that I was deceived in these cases. Once, too, the body appeared to be double, as in a bicephalous monster; it was attached to the bifid or forked root of the tail, and grew together or was connected along the middle line; this observation, however, was not so complete as to leave me free from doubts as to its absolute accuracy.

FIG. II.

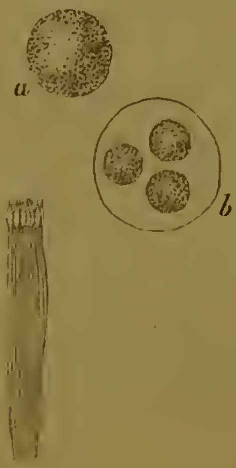

Fig. II.—Semen from the testicle of a man magnified from nine hundred to one thousand times:—*a*, a large roundish corpuscule; *b*, globule of evolution, a cyst which encloses three roundish granular bodies; *c*, a bundle of seminal animalcules, as they are grouped together in the testicle.

is therefore still more obtuse, superiorly and posteriorly, when seen from the side [10].

[10] The study of the varieties of form presented by the seminal animalcules ought not to be held as any trifling matter, or as tending to accumulate superfluous details; most important physiological conclusions may be based on the information thus acquired. Whether or not the varieties in point of size, and the more delicate shades of difference in regard to form, which are exhibited in the figures, are all constant, is a point still to be determined. In different individuals of the same species, the mole for example, we frequently observe varieties in the relative

Fig. III.

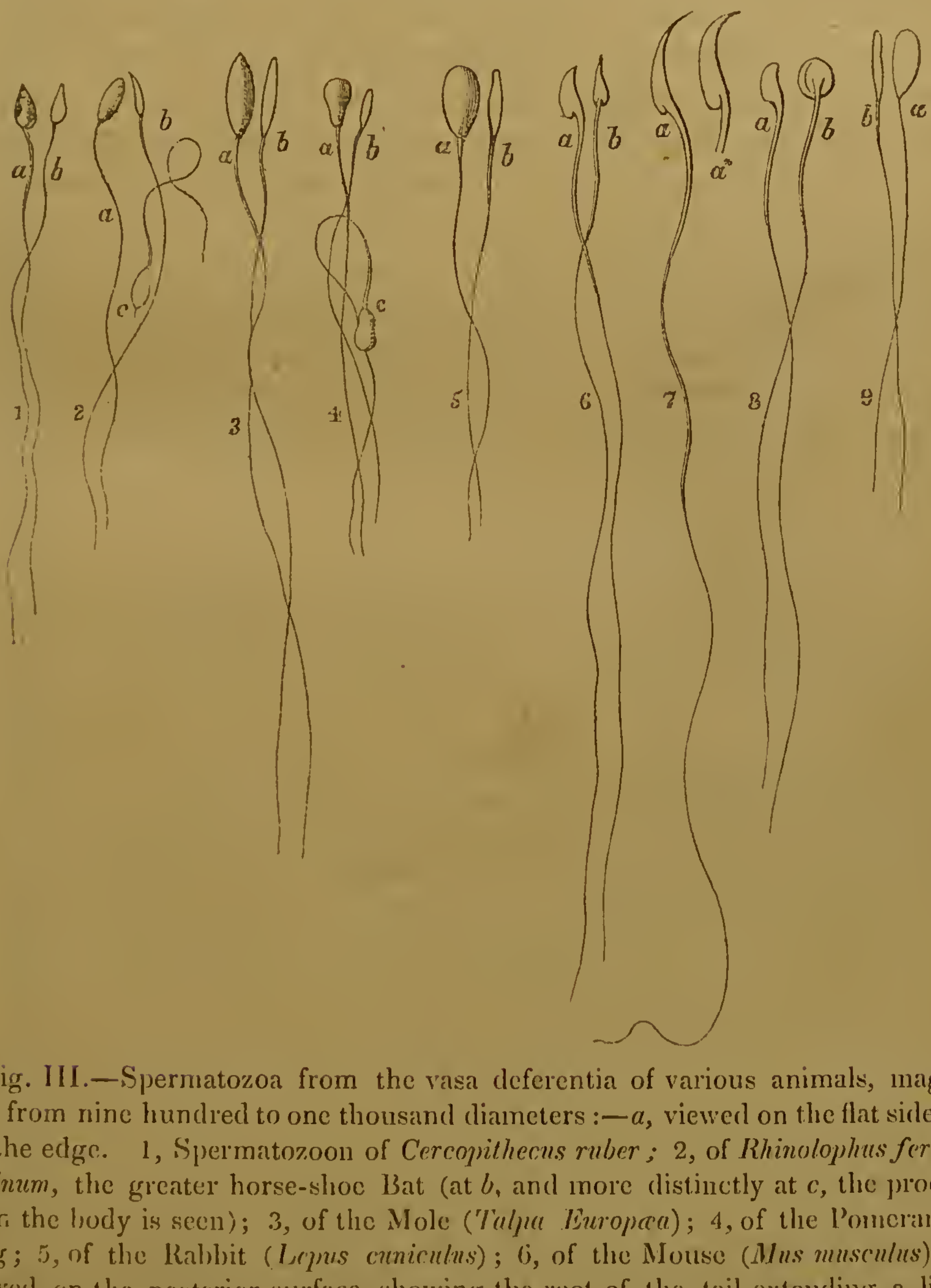

Fig. III.—Spermatozoa from the vasa deferentia of various animals, magnified from nine hundred to one thousand diameters :—*a*, viewed on the flat side; *b*, on the edge. 1, Spermatozoon of *Cercopithecus ruber;* 2, of *Rhinolophus ferrum equinum*, the greater horse-shoe Bat (at *b*, and more distinctly at *c*, the process from the body is seen); 3, of the Mole (*Talpa Europœa*); 4, of the Pomeranian Dog; 5, of the Rabbit (*Lepus cuniculus*); 6, of the Mouse (*Mus musculus*), *b*, viewed on the posterior surface, showing the root of the tail extending a little higher up; 7, of the Rat (*Mus rattus*); 8, of the Field Mouse (*Hypudæus arvalis*); 9, of the Roebuck (*Cervus capreolus*).

Among Birds two principal varieties are observed in the form of the spermatozoa: they have either a long slender body, perfectly cylindrical as it seems, with a tail extremely thin, filiform, and arising at once, not tapering off from the body, and once or twice as long again as this part; this appears to be the type in the Rapaces, Scansores, Gallinæ, Grallæ, and Palmipedes; or the cylindrical body is pointed anteriorly, and then makes several, generally from three to four, spiral turns, so that it resembles a corkscrew, and then tapers off gradually into a long straight tail, that grows smaller as it approaches its end. This is the type in the Passeres (fig. IV. *a, c, d, f, g*). The number of spiral turns, and the angle at which they proceed, are different in the different families and genera. The tail is of very dissimilar length and thickness. If the spiral be much drawn out and more sinuous in its appearance, the turns pass into each other under blunter angles, as in the Thrushes for example (fig. IV. *f.*); in the Shrikes (Laniadæ), again, the spiral is greatly contracted, and the turns appear almost acutely angular (*g*); the tail is here short and delicate, so that the whole animalcule measures but from the fiftieth to the sixtieth of a line in length; whilst in the Finches (Fringillidæ) they are much larger and stronger; in the Chaffinch, for instance (Fringilla cœlebs, fig. IV. *a*), they are the sixth of a line in length, the tail is very strong and rigid, and here, as among the Passeres generally, is never observed to move in the motions of the animalcule.

In the scaly families of the Amphibia, the lizards and serpents, the spermatozoa have for the most part an elongated body, and a delicate, filiform tail, like those of birds in general (*e. g.* the common

dimensions of the body of the spermatozoa; but this depends in part, at least, on the degree of dilution of the semen, on its freshness, on the degree of liveliness or power of motion, &c. &c. exhibited by these animalcules. The descriptions here given, and the forms presented, are all from spermatozoa in the most recent state possible. In beginning the study of the spermatozoa without assistance, I would particularly recommend the rodent tribes as the proper subjects, by reason of the magnitude and the decisive forms peculiar to their seminal animalcules. Let any one, for example, compare the seminal fluid of the mouse and rat, and he will immediately find that the spermatozoa of these two so closely allied animals present typical similarities not to be mistaken in the important matters of size, form of body, &c. &c. at the same time that they still exhibit specific differences adequate to distinguish them in every case from one another, and when they are contrasted. Other rodent animals, the squirrel, to cite a single case, have very peculiar and large spermatozoa, the margins of the body being turned up in some sort like the brim of a hat, &c. &c. Large animals, the horse, the ox, &c. have smaller and less specifically and obviously diversified spermatozoa, so that it is not so well to begin with these animals in analyzing the seminal fluid.

fowl, fig. IV. *i*). Those of the Frogs (Ranidæ) are of the same description; but among the other Batrachia, the greatest diversity

Fig. IV.

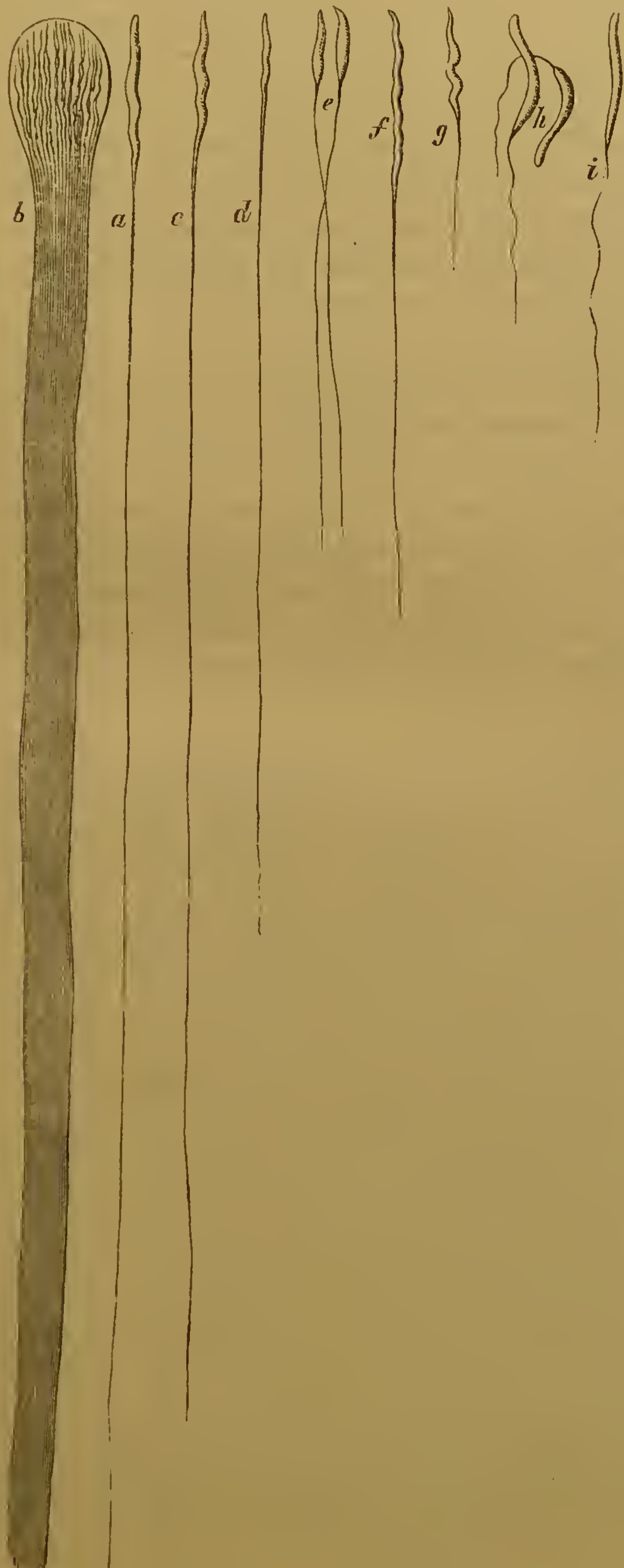

Fig. IV. — Spermatozoa from the vasa deferentia of several birds, magnified from nine hundred to one thousand diameters:—*a*, of *Fringilla cœlebs*; *b*, a perfectly formed cyst from the testicle of the same bird, containing a bundle of the spermatic animalcules; *c*, of *Fringilla canaria*; *d*, of *Fringilla carduelis*; *e*, imperfect spermatozoa from the testicle of a hybrid beween a male *Fringilla carduelis*, and a female *Fringilla canaria*; *f*, of *Turdus merula*; *g*, of *Lanius ruficus*; *h*, of *Picus viridis*; *i*, of *Gallus domesticus*.

of form prevails; those of the land and water Salamanders (Tritonidæ) may be cited as the most remarkable in this respect[11]. In this family the spermatozoa have a long body that tapers to a point anteriorly, and ends in a small tuber or button, from which issues a tail that becomes more slender as it proceeds, and of which the extremity is turned back, and is wound spirally several times about the whole body.

The spermatozoa of the Rays and Sharks among Cartilaginous Fishes, appear to be long and filiform; among bony fishes, again, their bodies are globular, sometimes provided with a projecting part or process, to which is attached a tail of considerable length, but so excessively delicate, that it is always discovered with difficulty.

The spermatozoa of the Invertebrata generally are elongated in their shape, hair-like, and extremely delicate; this is the case with the majority of insects. They have the same general characters, but are thicker and singularly long in the Mollusca; some of them are as much as half a line in length, and occasionally presenting a thicker and better developed extremity, which in certain cases, in the Mussel for instance, even assumes an oval form, they bear a very considerable resemblance to the spermatozoa of the Mammalia[12].

[11] The spermatozoa of singing birds form on these accounts very excellent subjects for initiatory observation. Specimens of singing birds of different genera and species are easily procured, too, for contrast, and I have therefore kept them particularly in view, both in the present and the next paragraph (§ 6). The vas deferens, divided in the vicinity of the cloaca, supplies us with the seminal fluid in abundance. How far the constant diversities of form in the spiral, and of size obtain, and how these bear relation to particular families of singing birds, and again, to particular species of them, requires to be made the subject of farther inquiry; the varieties indicated in reference to the shrike and finch, perhaps also to the thrush kinds, I am inclined to regard as family characters. It is remarkable, that all the birds without the singing muscular apparatus, which I have examined, which were formerly arranged in one order along with the true Passeres, and first detached from these by Nitszch—to wit, the genera Coracias, Caprimulgus, Alcedo, have not, any more than the Cuculidæ, Picidæ, and others of the Seansores order, the corkscrew-form of spermatozoa, whilst the Corvidæ, or crow-kinds, present precisely the same peculiarity in the constitution of their seminal animalcules as the true singing birds. Among the naked Amphibia, besides the land and water salamanders, the spermatozoa of which are very similar, yet different, the genera Bombinator and Pelobates have very peculiar seminal animalcules.

[12] The spermatozoa of the Invertebrata, however interesting they may be under other points of view, can only be briefly alluded to here, the investigation of the varieties of form, &c. described as occurring among mammalia and birds being

§ 6. A question of the greatest moment presents itself here, which, were it answered definitively, would leave no farther doubt in regard to the animal nature of the spermatozoa. It is this: Do the spermatozoa possess an internal organization, like the Entozoa and Infusoria? for the care and patienee of experienced observers, aided by the exeellenee of our modern instruments, have demonstrated, even in the smallest, and apparently simplest forms of the Infusoria, organs performing espeeial offiees, in partieular a eomplieated digestive apparatus. Opinions are greatly divided in regard to the way in whieh the question proposed must be answered. The spermatozoa were formerly referred to the Cereariæ, being named *Cercariæ Seminis*, and some most eareful observers of the present day defend the propriety of this disposition [13]. Some have thought, that in the middle of the flat bodies of the spermatozoa, even of the human subject, they could diseover a sugient orifiee, similar to that which exists in the Cercariæ and Distomata [14]; others will have it, that they ean make out ventrieular sacs, as in the polygastrie Infusoria [15]; and in direet opposition to all of these, there are others, who, with the highest magnifying powers, and the most anxious observation, have failed to pereeive, with any thing like eertainty, traees of internal organs in the transparent

sufficient to serve as grounds for the physiological conclusions immediately to be drawn, so that any farther detail seems unnecessary, and only likely to lead to confusion. Siebold has paid particular attention to the spermatozoa of insects, and described them minutely in the place already referred to. For an account of numerous other differences observable in the spermatozoa of various animals, I beg to refer to my *Aufsätze und Abhandlungen, im Denkschriften der Münchner Akademie,* and in Wiegmann's *Archiv,* Jahrg. 1836, 1837, 1838. I shall give a full account of all the known spermatozoa in the article Semen, in Todd's *Cyclopædia of Anatomy and Physiology.*

[13] That the manifold forms of spermatozoa, which I have shown to occur in the seminal fluid of a great number of animals, must be viewed in the light of so many different species, in case their animal nature is ever demonstrated, cannot be doubted; so that the expression *Cercaria Seminis* is only a collective title.—Vide Wiegmann's *Handbuch der Zoologie,* S. 584. Ehrenberg has also lately referred the seminal animalcules to the haustellate Entozoa.—Vide his recent great work, *Die Infusionsthierchen, &c.* fol. Leipz. 1838.

[14] Henle and Schwann recognize a middle sugient depression in human spermatozoa; it is undoubtedly the spot or macula described in the text to which they refer. Wiegmann, however, informs us, (*Archiv,* Bd. II. S. 134, 1837), that Henle has now abandoned this idea.

[15] Valentin speaks in various places of the polygastric structure of the spermatozoa, and says lately (*Repertorium,* 1837, S. 134), that "the clear spermatozoa of the bear, which in external form approach those of the rabbit, present distinct

bodies of the spermatozoa [16]. The excessively delicate or criniform spermatozoa of the invertebrate classes, resemble crystalline threads, without any kind of visible structure; neither in, nor on these, is there a trace of cellular, granular, or fibrous tissue to be detected. Those spermatozoa, however, which have a thicker or broader body—a part different from that which is filiform, do exhibit in this part the appearance of a fine granular tissue, which, under the highest magnifying powers that have yet been attained, cannot be decompounded into cells or other elements. Here, too, in the middle of the flat surface of the animalcule, a minute speck or spot, which often presents itself in the guise of a ring or a semicircle, is occasionally observed. This is the spot which has been pointed out by some as the suctory or absorbing orifice. This spot is represented in the seminal animalcule of the human subject in fig. I. *c*, *c*, (p. 8), and in that of the dog in fig. III. 4, *a*. (p. 11). Now and then, also, but by no means constantly, a small prominence or trunk-like process is observed on the anterior part of the body of the human spermatozoon (fig. I. *d*, p. 8); this, or a corresponding part, is more obviously, and much more regularly present in the seminal animalcule of the bat, in which it

traces of internal organization, to wit, an interior and posterior haustellate mouth, and internal cavities or convolutions of an intestine."

[16] The most varied, repeated, and long-continued examination has not enabled me at any time to discover true internal organs in the spermatozoa; and one of the most laborious and accurate observers of these animalcules, as well as most learned investigators of the more delicate structure of the entozoa, Dr. S. Siebold, coincides entirely in my views. (Siebold, in Wiegmann's *Archiv*, f. 1838, I. S. 303.) All that I have ever been able to make out is comprised in the statements in the text. Vide farther my remarks on the suspected organs of the spermatozoa, in my *Fragmente zur Physiologie der Zeugung*, S. 406. The darker-coloured macula bearing some resemblance to a haustellate orifice, I have now and then perceived in other spermatozoa, in those of the rabbit for example. The apparent spine implanted anteriorly on the body of the spermatozoon of *Rhinolophus* is by no means constant, and is never so distinctly seen, but that doubts of its import mingle with our observations of its existence; if it be an actual styliform process, the structure recalls that peculiarity which was first described by me in the cercaria armata. (Vide *Isis*, Jahrg. 1834, S. 131; and farther, Siebold, in Burdach's *Physiologie*, Bd. II. S. 192. 2te. Aufl.) I would here observe generally, that the nomenclature adopted in regard to the spermatozoa, such as body, head, tail, &c. is merely provisional, and will be either confirmed in its propriety, or rejected when farther progress is made in our knowledge of the minute anatomy of these corpuscules,—when the true import of the several parts that enter into their constitution shall have been discovered. It is not impossible but that, as in the case of the trichocephalus, the thinner filiform extremity which we at present entitle tail, may be found to be the head, &c. &c.

occurs as a pointed spine (fig. III. 2. *b c*, p. 11). Finally, the conjectural spermatozoa of the actinæ, exhibit evidence of a compound structure, but which is also capable of being interpreted in another way [17]. On reviewing all that has just been said, it is plain that at the present time no decisive answer can be given to the question regarding the animal organization of the spermatozoa. All that is yet known, or has been presumed upon the matter, reduces itself to this: that certain indistinct traces of organization have been discovered, but that these are by no means sufficient to be made the grounds of any positive conclusions.

§ 7. In what light are we to view the motions of the spermatozoa, and how are they effected? Have they any character of volition, and can any inference be drawn from their undoubted occurrence favourable to the idea of the independent animal nature of these bodies? These questions deserve the most careful consideration. To observe and compare the phenomena that accompany the motions of the spermatozoa, they must be studied under a variety of circumstances. When a drop of thick semen from the vas deferens, properly spread upon a piece of glass, is brought under the microscope, it frequently happens, even when the semen employed possesses considerable vitality, that nothing more than a general sluggish intestine movement is visible amid the crowded masses or heaps of spermatozoa. The appearance is as if they strove to disentangle themselves from one another in the tenacious fluid. If a little serum of the blood be now added to the drop of semen, the motions speedily become more lively; sometimes this happens suddenly, sometimes more gradually. Individual animalcules shake themselves once or twice, turn on their axis, strike with the tail, toss the head extremity once or oftener, and begin to make their way in all directions across the field; the motion extends to continually increasing numbers of other animalcules in succession; here and there every one of a cluster seems to arouse itself simultaneously; or otherwise, only a few that lie near each other in the mass put

[17] On the spermatozoa of the actiniæ, see my memoir in Wiegmann's *Archiv*, f. 1835, Bd. II. S. 215. I formerly believed that I had found spermatozoa having very peculiar characters in those organs of the actiniæ which are generally regarded as testicles: elongated, yet thick bodies, which suddenly throw out a filiform very long tail, which appeared to have been inclosed spirally within the body. Analogy and farther study lead me to doubt of the accuracy of the opinions I then formed. May not the oval bodies in question be capsules or cysts, in which the true spermatozoa, extremely elongated and filiform, are developed, and out of which they make their exit in the form of tails? This view I am at present inclined to think maintainable.

themselves in motion, whilst the rest seem to lie passive, and sometimes will continue so through the whole course of the observation, though frequently, too, they begin at length to stir in a greater or less degree, like those that first awoke. The motion in the globule of semen, thus attenuated with serum, appears throughout to have the character of regularity, certainly not of anything violent or forced; it is modified according to the form and dimensions of the spermatozoa; is the motion rapid, then the spermatozoa, as in the greater number of mammalia, bony fishes, acephala, &c., exhibit a pendulum-like rhythmical movement, the criniform tail vibrates vigorously like a whip, and the little body or head obeys the impulse thus communicated to it. When the motion is slower, a kind of serpentine or sinuous vibration of the tail in all directions is apparent. The rigid, straight, outstretched spermatozoa of the passeres, with spiral bodies, very commonly spin themselves round on their axis, and so advance in the manner of a piercer or screw; then they rest, and again they strike to the side, and advance in different directions, with a wavering and unsteady motion. The spermatozoa, with elongated cylindrical bodies and slender tails, like those of the other families of birds, of frogs, &c., scull themselves forward with their tails, either striking them slowly, and with wide sinuosities, or more quickly and shortly, as when a whip is shaken; they thus advance in circles with a quivering motion, holding the body extended in a straight line, though they also now and then bend this in various directions from side to side. The spermatozoa of the salamanders and tritons commonly lie coiled up in a circle like a watch-spring; then there arises a jerking tremulous movement, in which they seem to spin round in a circle upon one point as a pivot; along with this there is a lively, glistering, and wavy motion, that recalls those movements of the mucous surfaces which are produced by cilia, but which, on attentive examination, are here seen to depend on a rapid rotatory or spinning movement of the very delicate tail wound spirally about the body. Some of these spermatozoa too are occasionally seen to stretch themselves out, and to cross the field of the microscope with slow serpentine motions[18]. The various

[18] At an earlier period of my investigations I believed that the glistering unsteady motions of the spermatozoa of the salamanders were the effect of a ciliary apparatus, and even dilated on this as a means of locomotion in my *Fragmente*, already quoted, (p. 394, tab. II. fig. XVII. *u.* XVIII.) Siebold was the first who correctly referred to the spiral disposition of the tail around the body as the cause of the phenomenon, (V. Froriep's *Neue Notizen*, Bd. II. S. 281, No. 40.) I have very lately fully satisfied myself of the accuracy of this view.

motions of the spermatozoa now collectively described may be taken as the normal movements of these animalcules deduced from numerous particular observations; they strikingly impress the mind of the observer from first to last with the idea of spontaneity or volition; we cannot, certainly, refer them either to the motions entitled molecular, or to those that are ciliary in their origin; neither are they the effects of actions produced by hygroscopic or any other simply physical influence [19]. They agree in every thing with the motions immediately to be described, which take place in the spermatozoa of the seminal fluid that has been mixed with other secretions in the act of ejaculation.

§ 8. The spermatozoa of the semen which has undergone natural dilution by admixture with mucus, the fluid of the prostate, &c. (and which may be procured for examination from animals that have just copulated,) exhibit motions similar to those described in the preceding section, with this difference, that here they are quicker and more powerful; the animalcules of a globule of this semen swim very rapidly, with a vibratory and tremulous motion across the field. Hours, and even days after the sexual act, they may be discovered still possessed of the same activity amidst the

[19] The various very remarkable movements here described must be particularly studied by the young physiologist, that he may be enabled to distinguish them, and be placed beyond the risk of being deceived. The purely mechanical motions that occur in the corpuscules of different kinds suspended in fluids, when placed upon the stage of the microscope, in consequence of the instrument not standing perfectly level, of the unequal pressure of the plate of glass or mica which covers the globule of fluid examined, or of the presence of air-bubbles, &c. &c. will soon be distinguished by beginners. The peculiar molecular motion first accurately described by Mr. Robert Brown, (*A brief Account of Microscopical Observations on the Particles in the Pollen of Plants, and on the general Existence of active Molecules in organic and inorganic Bodies*, 8vo, Lond. 1827,) is observed in a vast variety of substances when finely pulverized. The black pigment of the choroid coat of the eye affords perhaps the best of all subjects for its study. A little of this pigment from the eye of an ox exhibits the dancing motions, the attractions and repulsions of the finest particles that characterize the phenomenon in great perfection. The true cause of this movement appears to be purely physical, but it has not yet been quite satisfactorily explained. On the incessant currents that occur in fluids, see the observations of Mohl, in his *Physiologie der Gewächse*, Heft I. S. 31 (1834). The ciliary motions, of which particular mention will be made by-and-by, are the effect of small vibrating cilia or hairs, free towards their points, and attached to tegumentary surfaces by their bases. The phenomena of ciliary motion are conveniently studied on a piece of the gill or mantle of the common fresh water mussel.—(Vide Dr. Sharpey's excellent article Cilia, in Todd's *Cyclopædia of Anatomy and Physiology*, in which the whole of the facts connected with this curious subject are exposed.)

mucus of the vagina and uterus. Common mucus and saliva have no hurtful or repressing influence on the motions of spermatozoa [20]. Even in urine and in bile they continue active, though for a shorter period; occasionally the motions cease suddenly; the animalcules start, as it were, a few times, and then lie quite still; often, too, they seem affected with strong convulsive-like motions; these last are still more speedily induced by the admixture of pure water. In the majority of instances, when pure water is added to a drop of semen, there suddenly occurs a rapid movement, a sudden commotion in the whole mass of seminal animalcules; they shoot about in all directions, and individuals may be observed bending or twisting themselves violently, so that the tails frequently become entangled, and form knots. Shortly afterwards the whole mass becomes quiescent, although one here and there may still be observed to move, or to be twitched convulsively, and this sometimes very violently. A speedy addition of blood or serum is occasionally followed by the return of regular motions, which, however, are never of any duration. Weak solutions of sugar or of salt in water produce these powerful effects either in a less degree or not at all. The addition of a very small quantity of pure water, too, seems frequently to have no influence in arresting the motions of the spermatozoa; and it is remarkable, that these animalcules manifest very different susceptibilities to the action of water pure, or impregnated with some saline matter in different classes, and even

[20] Donné has performed a series of experiments on the influence of different animal fluids on the spermatozoa. (*Nouvelles Expériences sur les Animalcules Spermatiques*, Paris, 1837, 8vo.) Blood produced no ill effects on them; they will live for one, two, three, and even four hours, moving freely, rapidly, and without any loss of strength. Whether the blood employed was that of a man or of a cold-blooded animal, the effect was the same. The motions fall off in vivacity gradually, and the animalcules die without any violent or convulsive phenomena, and remain in the position in which they were previously. Milk has the same influence as blood; spermatozoa will live for hours in this fluid. Saliva destroys them quickly, and in their agony the tail is apt to form eyes or knots. In urine they perish instantaneously. In pus (from chancre and vaginal gonorrhœa) they appear to live as long as in the spermatic fluid itself. The mucus of the vagina is so weakly acid, that the spermatozoa do not seem to suffer from it, although in general they are less affected by fluids that are slightly alkalescent than by those that are in any way acid. These conclusions of Donné I have found correct on the whole; on particular points, however, my own experiments, instituted for the most part on the spermatozoa of the lower animals, led me to different conclusions: I found, for instance, that they almost always lived in saliva; also in urine, particularly when it was kept warm, and was not too concentrated; after a nocturnal emission, for example, although several hours have elapsed, feeble vital motions may still be perceived in the spermatozoa then con-

in different genera of animals [21]. Diluted acids, alcohol, and similar fluids, arrest the motions of the spermatozoa in the instant, and the creatures lie in all irregular positions, and altered in their forms upon the field. The effect of narcotic substances is particularly interesting; watery solutions of the salts of strychnia always arrest the motions suddenly; in general, too, they very soon cease under the influence of solutions of opium and of cherry-laurel water, but without any change in the form of the animalcules being induced [22].

§ 9. The normal duration of the motions of spermatozoa is different in different animals. It appears to be shortest in birds; among which within so short a time as from fifteen to twenty minutes after the death of the animal, it is frequently no longer to

tained in the urine. I have repeatedly detected them in the urine of persons whom I suspected of masturbation; also in urine that let fall a purulent sediment. [Dr. John Davy (*Edinb. Med. Surg. Journ.* vol. 50.) reports that, on examining the fluid from the urethra after stool in a healthy man, he had always detected spermatozoa in it. I have, under the same circumstances, and even after the mere evacuation of the bladder, several times discovered spermatozoa in the fluid of the urethra, but the subjects of my observation were never strong or healthy men; they mostly laboured under anomalous nervous symptoms, which were in all likelihood connected with an irritable or disordered state of the vesiculæ seminales and prostatic part of the urethra. R. W.]

[21] The addition of water almost invariably increases the motion in the first instance. The animalcules rush tumultuously past one another, and die off singly. The spermatozoa of the invertebrata, of amphibia, and mammalia, almost always form loops or eyes; those of the latter not invariably; those of birds again almost never. The spermatic fluid of fishes mixed with water exhibits a commotion that lasts many seconds, and even minutes; after which entire quiescence follows, or only individual animalcules stir. In the spermatic fluid of the common earthworm, the animalcules on the addition of water commove themselves in masses in a wavy manner, by which a singular and beautiful effect is produced, that might be compared to the waving motion of a corn field.

[22] The effect of even the weakest solution of strychnine is always sudden; when the whole of the animalcules in a diluted drop of semen are seen in full activity, all that the poisonous fluid reaches die immediately; the others in the immediate vicinity of these, which it has not attained, still continue to move vigorously. To secure the gradual contact of this solution, and to observe its effects, a piece of cotton or woollen-thread, or a narrow slip of filtering-paper, may be laid in the drop of seminal fluid under examination, and touched at one end with a glass rod dipped in the narcotic solution; by the capillary attraction of the thread or slip of paper the reagent penetrates the drop of semen slowly, and produces its specific effects gradually. I have found the influence of such a narcotic solution of a like potency upon the spermatozoa in mammalia, birds, and amphibia.

be perceived: this is particularly the case when the external temperature is low and the body cools quickly. Occasionally, nevertheless, motion is conspicuous, at least in regard to individual spermatozoa, some hours after the death of the bird from which they were derived[23].

In mammalia the spermatozoa continue to exhibit motion much longer, in some cases even at the end of twenty-four hours after the death of the animal. In amphibia this is still more remarkably the case; and in fishes, when the temperature is not too high, and putrefaction does not take place, the motions of the spermatozoa continue longer than in any other of the vertebrate classes. The spermatozoa continue alive much longer when the semen remains inclosed in its natural receptacles than when it has been taken out of these: this at least is the case in regard to the warm-blooded vertebrata; in fishes, as I have just said, they live on for several days, even out of the body[24].

In weak solutions of sugar and common salt, too, the spermatozoa of vertebrata continue active for six or eight hours; and those of man, after nocturnal emissions, may be found alive in the

[23] I have always observed the most rapid and lively movements among the spermatozoa of birds, particularly passeres of all kinds, killed by decapitation or strangulation. The whole mass of semen examined was alive and quivering, and the appearance it presented might be compared to a packet of sewing-needles shaken rapidly backwards and forwards and about; individual animalcules at the same time were spinning swiftly on their axes, and so on—facts which Siebold certainly does wrong in denying (Müller's *Archiv*, 1837, S. 436). In a single (and rare) instance, I observed the spermatozoa of a lark in motion eighteen hours after the death of the bird, the abdomen of which had also been opened. They may commonly enough be observed to move, in birds that have been shot, two or three hours after death.

[24] In rabbits, mice, &c. that have been killed the night before, the spermatozoa are commonly found alive next day: if a piece of the turgid vas deferens of one of these animals be put into serum or sugar-water, and a drop of spermatic fluid be added at the same time, the spermatozoa will usually be found to continue their motions in the fluid of the vas deferens for a long time after they have become quiescent in that of the added drop. I have found the spermatozoa of frogs, skinned and prepared for cooking, still in motion. Among fishes I have observed the spermatozoa to be singularly long-lived. I once kept a slender test-glass full of the spermatic fluid, obtained directly from the turgid testes of the common perch, for four days in cool weather, and found the animalcules as lively and disposed to comport themselves precisely in the same manner as those of the generality of animals but just killed; the motions were sluggish in the undiluted semen, but became singularly active on the addition of water; they then ceased of a sudden, &c.; they did not cease at a temperature two degrees below the freezing point of water.

urine hours afterwards[25]. Very low or very high temperatures have a like influence in arresting the motions of the spermatozoa; although those of frogs and fishes still continue active when the surrounding medium reaches, or even sinks below the freezing point. The kind of death which an animal suffers has no influence on the duration of the motions of its spermatozoa[26].

§ 10. *Production of the Spermatozoa.*

The genesis, or production and development of spermatozoa are subjects of much interest, and very remarkable; both take place through the entire series of animals after a very similar type, which presents but slight modifications. For the study of this subject, a bird, and that one of the order of Passeres, should be chosen; the circumstance of the pairing time in these creatures being so determinately attached to a certain season, affords us an opportunity of watching the genesis and evolution of their spermatozoa in the most clear and satisfactory manner. The testes themselves, according to their condition, always prefigure the state of evolution of the spermatozoa. In winter the testes present themselves as a couple of small bodies, the size of a pin's head, or a millet-seed; the seminal vessels are then exceeedingly contracted, but still demonstrable as tortuous canals, lined with an epithelium. Whether the very minute granular bodies, from the $\frac{1}{300}$th to the $\frac{1}{400}$th of a line in diameter, which are then contained in their interior, be of a peculiar nature, or belong to the epithelium, is doubtful. With the advance of spring, the testes gradually increase in size, and at length are found of twenty, and even thirty times the size and weight they possessed in the depth of winter[27]. The seminal

[25] Refer back to the observations on the preceding paragraph (§ 8) Annot. 20, 21, 22.

[26] It seemed to be perfectly indifferent in what manner the animals were killed whose seminal animalcules I wished to examine; dogs, rabbits, birds, &c. poisoned with strychnine, coniine, &c., the irritability of whose muscular nerves was entirely gone, still afforded me spermatozoa possessed of all their activity, which lasted as long, too, as under any other circumstances.

[27] The testicles become of extraordinary magnitude, both absolutely and in relation to the rest of the body, in the duck, and in the common fowl; in the passeres, or singing birds, I also find them very remarkably developed, and the left testis generally more so than the right. On this subject see my *Elements of Comparative Anatomy (Lehrb. der vergleichenden Anatomie*, S. 248), and my *Contributions to the Anatomy of Birds (Beiträge zur Anatomie der Vögel)*, in the *Abhandlungen der Baierischen Akademie*, Bd. II. S. 284. The progressive enlargement of the testis in birds as the pairing time approached, was studied by Mr.

vessels expand greatly and form thick convolutions like those of the brain, visible to the naked eye, and glistering through the proper capsule of the testis, which is now covered with a network of arteries and veins. At first, granules and globules of different sizes and forms, either more darkly granular, or pale with several larger molecules included, and frequently with only a single larger granule in the centre, are discovered (fig. V. *a*, *b*). These cor-

Hunter (vide *Animal Œconomy*, ed. by Owen, 1837, 8vo), and plans of their relative dimensions in the House-sparrow at different seasons, are given by Owen in his article Aves in Todd's *Cyclopædia*, vol. I. p. 354.

Fig. V.

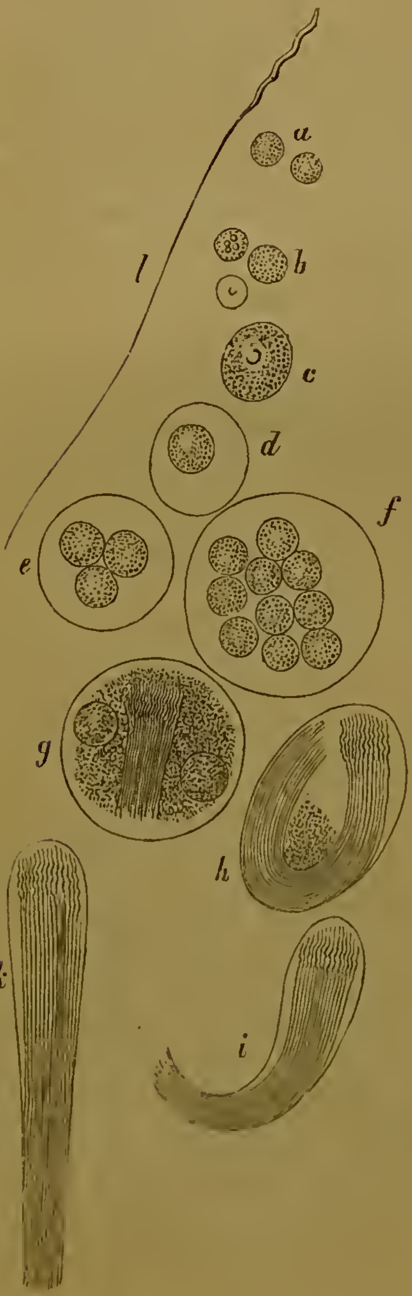

Fig. V.—This fig. represents the several stages of evolution of the spermatic animalcules of *certhia familiaris* (common creeper). As a greater degree of force has been given to the outline than is to be met with in nature, the figure rather resembles a plan than an exact copy of what may be observed. The objects are delineated as magnified from nine hundred to one thousand times:—*l*, an adult spermatozoon taken from the orifice of the vas deferens; *a*, seminal granules, taken from a very collapsed testicle in the winter season; *b—k*, several seminal granules, taken from a testicle in summer, during turgescence; *b*, *c*, seminal granules, which are probably nothing more than altered epithelial cells; *d*, *e*, *f*, cysts or vesicles, enclosing one or more round granular globules; *g*, a similar cyst, containing, besides the two globules, a finely granular mass, in which the spermatozoa may be seen to form; *h*, the cyst, still containing some finely granular matter, has assumed an oval form, and the bundle of spermatic animalcules, increased in size, lies bent up within it; *i*, a cyst still more developed, the involucrum, pear-shaped, covers the bundle of animalcules where their spiral extremities lie; *k*, a cyst arrived at maturity, still covered by the involucrum.

puscules or globules are from the $\frac{1}{200}$th to the $\frac{1}{300}$th of a line in diameter. One of the larger darker globules, with evident traces of a central nucleus, is here represented (fig. V. *c*). Whether these globules are new elements, or altered epithelium-cells, it is difficult to determine. No less so is it to say whether they undergo transformation or evolution in the manner of the bodies next to be described, by assuming a covering, or expanding bladderwise involved in a dense tunica propria. Along with these bodies, and in connexion with the increasing afflux of blood, and augmenting turgescence of the testes, there are evolved numbers of distinctly rounded and perfectly transparent vesicles, which at first present one (fig. V. *d*), and then several,—two, three, four (*e*), and as many as ten and more nuclei. These nuclei are delicate, pale, (in the figure they are too dark and hard,) granulated globules, bearing a partial resemblance to the finer globules (*a*) first described. The vesicles, or replete globules, now under consideration, grow from the $\frac{1}{150}$th to the $\frac{1}{100}$th, and finally to the $\frac{1}{50}$th of a line in diameter. In the course of their development a fine granular precipitate is observed to form between the included nuclei, by which these are first obscured and then made to disappear, and linear groupings are produced, which anon proclaim themselves as bundles of spermatozoa, already recognizable by slight traces of a spiral formation of one extremity (fig. V. *g*). It were hard to say whether the finely granular precipitate is to be regarded as the product of a process of resolution occurring to the nuclei, or a new formation, as also, whether the spermatozoa spring out of, or only in and amidst this yolk-like matter, or matter that at all events is comparable to the yolk of eggs in general. The vesicles now assume an oval form (fig. V. *h*), the globules disappear, the granular contents diminish; the seminal animalcules are well-grown, and lie bent up within the cyst; their spiral ends are more conspicuous. The delicate covering (involucrum) is now drawn more closely around the bundle of spermatozoa it includes, and where it covers their spiral ends anteriorly it assumes a pyriform outline (*i*), and at the opposite extremity is perhaps at this time open; but it is difficult to speak decisively on this point. The cysts are now very commonly bent nearly at right angles, or like knees; but at length they appear stretched out and straight, and have attained their full size (*k*). The capsules of these vesicles are at all times, and especially towards the end of their existence, highly hygroscopic: the addition of a little water causes them to burst, the masses of spermatozoa, rolled up like a little skein of thread or silk, escape, and occasionally at this stage exhibit motions individually, which, how-

ever, whilst the animalcules continue in the ducts of the testes, are frequently not to be observed, and are never either general or remarkable. The spermatozoa, after the rupture of the cyst, advance in freedom to the vas deferens, where they become stronger, and commonly look as if they were better nourished (fig. I.); severally the spermatozoa are here about the $\frac{1}{30}$th of a line in length, and the fully developed cysts and bundles (fig. V. *k*) in the testicle have the same dimensions; it is at this period that, from their lying many together, they can be most easily followed to their smaller ends, and most advantageously subjected to micrometric admeasurement. The spermatozoa of the finches (fringillidæ) are extremely large, particularly in the bullfinch, where they are as much as the $\frac{1}{6}$th of a line in length (fig. IV. *b*). In other families, as in the laniadæ, they remain much shorter; they are still shorter and far more globular in all the remaining families of the class [28]. It is equally easy to follow the several steps in the development of the spermatozoa in cysts and vesicles among the frog tribes; but more difficult to observe them in the mammalia and man; in whom, nevertheless, precisely similar bodies, and what may be called vesicles of evolution, present themselves (fig. II. *a*, *b*, from the human subject), as also aggregated bundles or skeins of spermatozoa (fig. II. *c*), the covering of which appears to be of extraordinary delicacy. Besides these granules, vesicles and bundles of spermatozoa, and intermingled with them numerous scales of epithelium are conspicuous, and not unfrequently oil-globules in greater or smaller numbers (fig. VI.) And then there is the liquor

[28] On the development of the spermatozoa in the yellow-hammer, similar in every particular to that in birds generally, vide my paper in Müller's *Archiv* für 1836, S. 225, and of those of the pigeon, vide my *Fragments on the Physiology of Generation (Fragmente zur Physiologie der Zeugung*, Tab. I. S. 388). In the mammalia, amphibia, &c. I have rather frequently found spermatozoa in the testis endowed with the capacity of motion to a considerable degree.

FIG. VI.

FIG. VI.—Seminal fluid of the rabbit:—A, from the vas deferens; *a* and *b*, two pale, flat, finely granular bodies, which, I take it, are merely epithelial scales; *c*, two bodies, more opaque, and having darker outlines, which I regard as true seminal granules; *d*, *d*, blood-globules for contrast, one is seen edgewise; *e*, seminal animalcule. B, seminal fluid from the testis:—*a* and *b*, two very dark

seminis as the vehicle of the whole. This is now a perfectly transparent crystalline fluid; and again it is turbid, and crowded with excessively minute molecules, very similar to the fovilla of the pollen-granules of plants. These delicate pale molecules, which are under the $\frac{1}{1000}$th of a line in diameter, exhibit the common molecular movement [29].

§ 11. The spermatozoa of the mammalia in the rutting season, and of young animals in general when they become capable of reproduction—man as he attains puberty inclusive—are developed precisely in the same manner as in birds at the pairing time. A larger quantity of blood is sent to the testes, these organs enlarge, the parietes of the seminal canals become thicker, the diameter of their area increases, and they are distended with granules; by and by the cysts or cells with their included globules as

[29] In reviewing the history of the evolution of the spermatozoa now given, in connexion with the discoveries of Schleiden and Schwann on the development of vegetables and animals alike from cells (see farther on this subject under our head of DEVELOPMENT), the idea presents itself to the mind whether the liquor seminis is not to be regarded as a "matrix" (Zellenkeimstoff, Cytoblastema, *Schwann)*, in which the granular nuclei are developed as *cytoblasts*, which again put forth their covering or cyst as a cellular wall: the finely granular contents would then have to be considered as the *cell-fluid*. The cytoblasts disappear so soon as the spermatozoa are evolved in their contents, and the cells burst and cast out the animalcules as the cells of the algæ scatter abroad their sporules. It would be desirable to inquire farther into this matter, and endeavour to discover whether the cell-nuclei, or globules of the vesicles, also contain corpuscules as nuclei in their interior, which they very obviously appear to do occasionally, (fig. VII.)

and well defined bodies, which I imagine to be oil-globules; *c, c*, a cluster of four much smaller, but very well defined corpuscles, probably also oil-globules; *d* and *e*, two pale granular bodies of different sizes, either seminal granules or epithelial scales; *f*, another body of the same kind, but darker; *g* and *h*, evolution globules or cysts, with a number of extremely pale globules and some granular matter included. [Dr. John Davy, in the testes of man, invariably found extremely minute dense spherules, which he conjectures to be the ova of the spermatozoa. *Researches*, v. i. p. 332. R. W.]

FIG. VII.

Fig. VII.—A very large cyst or bladder of evolution, containing five extremely pale globules, each of which exhibits a very minute dark nucleus. This appearance is extremely rare; it was met with in the seminal fluid of the *lanius ruficeps*; *b*, two seminal granules from the vas deferens.

nuclei make their appearance, and in these the spermatozoa are evolved[30].

The spermatozoa attain their highest development and motility in the excretory duct or epididymis [31]. So also in very advanced age, or as a consequence of local or general disease, and among animals living in a state of nature at all seasons save that of rutting, we commonly find the vasa deferentia empty and contracted[32], the seminal vessels of the testes small and only containing granules and here and there a globule of fat. This retrogressive process may likewise be very readily followed step by step among the tribe of singing-birds (passeres). After one or two broods have been hatched in the spring, about the middle or end of summer the

[30] It is thus that they occur in lads at the age of puberty, in young mammalia generally, and in birds. In the rabbit the spermatozoa are developed at a very early age: by the end of the third month from birth they are found to have attained complete maturity. In the dog and cat they are only developed at a much later period.

[31] This circumstance already alluded to oftener than once, namely, the more perfect development of the spermatozoa in the epididymis and vas deferens than in the testis, can only be fully appreciated on a careful inspection of these animalcules; properly speaking, they are not perhaps absolutely larger, but they are more distinct and plump, presenting a sharper outline, and looking altogether as if they were better nourished.

[32] In men in the flower of their age, and in animals during their season of heat, the capacity of the vas deferens is increased, its walls are attenuated, and the spermatic fluid escapes, or is readily pressed out from its interior when it is cut across, in the shape of a milk-white drop of fluid. In men between sixty and seventy years of age, I have still found spermatozoa in the seminal canals of the testicle; in the vas deferens they were not numerous; in the vesiculæ seminales they seemed to be in the ordinary numbers. The walls of the vas deferens in old age acquire an almost cartilaginous degree of hardness, the diameter of its canal is much reduced, or nearly obliterated; in some cases the walls appeared actually to have coalesced. It is very commonly reported that exhausting diseases, and mental emotions of a depressing kind when long-continued, cause a disappearance of the seminal animalcules. But I have found them very rife under such circumstances: they occur in abundance in cases of confirmed phthisis, and in subjects worn out with hectic fever; they are always abundant in individuals who have died by the hand of justice, as well as in those who have laid violent hands on themselves. I do not know whether or not they are wanting after violent nervous attacks, after typhus, tabes dorsalis, &c.; a point which would be interesting to ascertain In one case of a youthful and strong man, in which the testicle had been extirpated on account of disease, I failed to discover any spermatozoa, although by the side of the abscesses and fistulous passages there were many perfectly healthy portions of the testis remaining, with the seminal ducts quite normal. I have also occasionally missed spermatozoa in the proper passages of aged, much emaciated, and sickly dogs. Dr. John Davy, in eighteen out of twenty cases, found spermatozoa in the dead bodies of men who had died of very different diseases. (*Edinb. Med. and Surg. Journ.* vol. 50. p. 1.)

moulting season begins; at this time the testicles have already very much contracted, and they become smaller every day. The vasa deferentia, the ends of which formed club-shaped masses by the side of or behind the cloaca at an earlier period little inferior in size to the testes themselves, still contain seminal fluid in small quantity; but the spermatozoa are motionless and pining; their spiral-shaped ends are still distinguishable, but the windings appear more like knots. In the testes the nucleated vesicles or evolution-globules are very few in number, and by and by disappear entirely; the smaller granules, and the bodies which are perhaps to be regarded as altered epithelial cells, are still present, and among them a certain number of obviously shrivelled cysts, in which the spermatozoa appear to have suffered an arrest of development, and never to have come to maturity, as if they had been produced unnecessarily and were never to be used; the spermatozoa in these do not now lie in masses or bundles, but singly, apart, altered in character, and only partially exhibiting the spiral extremity; mixed with the spermatozoa there are also certain yellowish globules, which refract the light powerfully, molecules about the $\frac{1}{800}$th of a line in diameter, and not unlike oil-globules in appearance. Somewhat later, these cysts, now plainly involved in the general degeneration, are no longer to be found, but in their stead, and perhaps proceeding out of them, certain globular or oval bodies, from the $\frac{1}{100}$th to the $\frac{1}{150}$th of a line in diameter, and aggregates of large dark round-shaped molecules or granules, now and then with a somewhat clearer nucleus, which are comparable in some sort with the large pigmentary aggregates or bodies that occur in the choroid coat of the eye. In the testis itself there is no more trace of spermatozoa to be found, than in the vas deferens[33].

[33] I have not thought proper to follow out the history of the decay or degeneration of the spermatozoa with the same extent of detail as that of their development, so that their states at various intermediate times are not noticed, and perhaps other particulars not without interest are overlooked. The crow and magpie were the principal subjects of my observations in this part of the inquiry, and it is from these that the particulars in the text are given. It is to be understood of course that all the facts there set down were not observed in the precise order in which they appear, that the account rendered of them is always an epitome of many isolated observations, and even connected and completed in parts by analogy; though individual adventitious points may be called in question, and my explanations of others may even be shown to be erroneous, I still believe nevertheless that I can vouch for the accuracy of all that is essential. The whole of my statements rest on my own very numerous observations and researches; as weighty guarantees of their accuracy, I am happy in being able to cite Siebold (in Müller's *Archiv*, 1836, S. 436), and Valentin (in his *Repertorium*, 1837, S. 143).

§ 12. *Examination of the Male Sexual Organs of Hybrids.*

It is an universal law in natural history that animals of the same species only seek sexual intercourse spontaneously, and give birth to a fruitful progeny. It is perhaps only under some artificial influence, usually traceable to the interference of man, that animals of different species intermingle sexually: in their natural state of freedom an union of this kind certainly occurs very rarely, and it is only between generically allied animals that such a conjunction has any sequence; the *mules* or *hybrids* then produced are for the most part barren, or otherwise they are capable of procreating with one or other of the animals from which they are descended through at most one generation; two mules have very seldom been known to have fruitful intercourse; the race then dies out. This fixed law, ordained for the protection and continuance of existing kinds and species, is of the highest importance[34], and naturally leads to the question as to the state of the germ-preparing sexual organs of the males of mules, whether spermatic fluid is produced, and whether spermatozoa are present in the fluid secreted. Several isolated observations would

[34] A comprehensive general view of all the trustworthy accounts yet published in regard to hybrids of the higher animals, which have either been produced under the dominion of man, or been encountered in the natural wild state, would be of great physiological interest; particularly if a careful comparison were at the same time given of the colour, and of any peculiarities of external conformation and internal structure, the comparison being made as well between the animals of the parent stock as between the hybrids themselves. Undoubted cases of hybridism are almost only known as having occurred between animals that belong to one genus,—for example, between the wolf and the dog, the lion and tiger, the sheep and goat, the horse and ass, the horse and zebra, &c. All of these animals only communicate sexually under the influence and with the interference of man; and they are even then for the most part brought to copulate with difficulty. Exceptions to the rule of identity of genus being necessary to the production of hybrids, are of exceeding variety; still there have been cases of fruitful intercourse occurring between the goat and chamois, and even between the sheep and roe; the old tales of productive intercourse between man and animals, and between animals of extremely different kinds, are altogether unworthy of credit. Barrenness is the appanage of hybridism; they are exceptions, and extremely rare exceptions, where hybrid animals prove fruitful with individuals of the original stock. Upon this subject I beg to refer to Burdach's *Physiologie*, Bd. I. S. 511. (tom. ii. p. 182. of Jourdan's French translation,) and the excellent critical remarks on the hybrids of the genus *equus* and *ovis*, by Andrew Wagner, in Schreber's *Säugethieren*, Bd. VI. S. 185, and Bd. V. 1281 et seq On the hybrids of birds, see observations under annotation 36. Instances of the production of hybrids are also known to have occurred among amphibia, fishes, and invertebrate animals. Vide *Burdach*, loc. cit.

lead to the conclusion that the semen of the mule, at least of that proceeding from the horse and ass, contains no spermatozoa[35]. In the difficulty which is felt in these countries of procuring the mules of mammalia as subjects for a series of observations, it is more convenient and much easier to make use of the mule progeny of birds. Those that are most commonly met with are the hybrids of canary-birds, and others of the finch tribe, such as the goldfinch, gray-linnet, &c.[36] It is well known that many of these mule

[35] Hebenstreit, Bonnet, and Von Gleichen, all inform us that they had failed to discover spermatozoa in the stallion of the common mule, or hybrid between the mare and ass; Prevost and Dumas, whose observations bear the impress of accuracy and authenticity, found no trace of seminal animalcule in the whole course of the genital organs of a male mule, which was remarkable for its salaciousness; the contents of the seminal canals, of the testes, and vasa deferentia, consisted of globules only (the figures prove them to have been mere epithelial cells); in a horse and ass examined at the same time, plenty of spermatozoa were discovered. Vide their paper in *Ann. des Sciences Naturelles*, I. p. 182, and Pl. 12, C. A. M.

[36] Here also I choose birds as the subjects of my inquiries; among which decisive observations are easily and at any time repeated. It is remarkable and doubly interesting that it is among birds, and particularly gallinaceous birds, that hybrid productions occur more commonly perhaps than among all the other classes of animals put together. The number of instances increases every day in which the *tetrao tetrix* (moorfowl) and the *tetrao urogallus* (blackcock) have been found to have fruitful connexion in their natural wild state, the product of this union being the *tetrao medius*, long regarded by naturalists as a distinct species. On this subject see Naumann's *Natural History of the Birds of Germany (Naturgeschichte der Vögel Deutschlands*, B. VI. S. 304,) and Gloger's *Manual of the Natural History of the Birds of Europe (Handbuch der Naturgeschichte der Vögel Europas*, I. S. 512). In Sweden and Russia such instances seem to occur still more frequently. I had myself, very lately, a specimen from the south of Bavaria, but was unfortunately prevented from examining the sexual organs. The instances of a productive union between the *tetrao tetrix* (moorfowl) and the *tetrao lagopus* (ptarmigan) in their natural state of freedom, are of rarer occurrence; as also of the *hirundo domestica* (house-swallow) and the *hirundo agrestis* (marten), cases of which will be found recorded by Naumann and Gloger. Numerous instances have occurred of hybrids between the pheasant and common domestic fowl, as also between different members of the pheasant family with one another; these hybrids are almost always barren, occasionally only are they capable of engendering. Breeders of canary-birds have found that these creatures engender readily enough with the goldfinch, linnet, and siskin, and with greater difficulty with the greenfinch and chaffinch; whether they will procreate with the yellowhammer *(emberiza citrinella)* or not is doubtful; I find no accounts that can be depended upon on this point: if fruitful connexion did occur, it would be particularly remarkable on account of the generic difference of the kinds. In general these hybrids are barren; there are, however, undoubted instances on record in which mules, both male and female, of the gold-

birds can never be brought to pair at all; that the pairing of others, when it does take place, remains unproductive, and that some few only pair and engender. It must therefore be extremely interesting to examine the contents of the testes in such birds, to observe the changes which their sexual organs undergo in the course of the spring, and to contrast these with the corresponding parts in the original stock-birds. The male of the canary comports itself in all respects like the other passeres: the testes enlarge by degrees to rounded oval bodies of considerable magnitude, and generally of somewhat unequal size; the vasa deferentia form peculiar club-shaped convoluted masses on either side of the cloaca; the spermatozoa contained in these, as in all the other members of the finch family, are very large and strong, though somewhat less so than those of the chaffinch, and about the tenth of a line in length; their spiral end is well developed and furnished with two principal threads (fig. IV. *c*) of the screw. In the male goldfinch, every circumstance bears the same general complexion, but even the best developed of the spermatozoa are here somewhat more slender and shorter; their spiral end, too, is less strongly marked (fig. IV. *d*); they measure the $\frac{1}{15}$th of a line in length. The sexual organs of the male mule or hybrid of the male goldfinch and female canary, exhibit great diversities in the state of development of the testicles at the pairing season. In some, these organs continue extremely small; in others they enlarge in different degrees, but scarcely ever attain to more than half the size of those of the stockbird, and are always of a rounder form; they are either

finch and canary have shown themselves capable of procreation; but this was only with canary-birds, as it would appear, not with one another. I have sacrificed a considerable number of hybrids of this kind in the course of my inquiries on the subject of generation; I always found the vasa deferentia empty: in the testicles the product varied; there were either no seminal animalcules discovered or these were imperfectly developed. I imagine, however, that hybrids actually capable of engendering must produce proper spermatozoa. In female hybrids I found all the anatomical requisites to procreation; to wit, an oviduct, an ovary with numerous little yolks which all contained a germinal vesicle; I never saw ripe or ripening yolks, however. It were of the highest interest for natural history in general, as well as the physiology of generation, were an extensive and systematic series of observations, which should be varied in every possible manner, and repeated again and again, to be undertaken upon the crossings and intermixtures of our cage-birds and their hybrids. The facility with which canary-birds are reared, and the readiness with which they admit birds of other kinds to their society, seem to promise the best results in taking them as the subjects of observation. Continued researches in minute anatomy would necessarily go hand-in-hand with these observations.

developed in equal measures, or the one grows more than the other; sometimes the right, sometimes the left. In those that are best developed, the windings of the seminal canals, and the beautiful network of blood-vessels, are distinctly seen shining through the tunica propria. The fluid contained in these canals is white, and presents globules and granules of different sizes, similar to those discovered in the testes of other birds (fig. V. *a*—*c*), but the true, the proper genetic globules are always wanting. Instead of these we meet with roundish and elongated globules and bladders, from the $\frac{1}{100}$th to the $\frac{1}{40}$th of a line in length, filled internally with small dark molecules, occasionally with clear rings including bodies that look like germinal vesicles; many of these corpuscules are elongated and pyriform, and inclose threads with dilated extremities; but these are never connected into regular bundles, are always less numerous, and lie irregularly between or among the molecules, which are darker and larger than in the granular matter of the genuine cyst of the seminal animalcule. These formations seem to depend on and to denote an imperfect production of spermatozoa, which are entirely wanting in many mules; when they do occur, they are always at the best smaller than those of the stock-bird, measuring the twenty-fifth, at the very most the twentieth of a line in length. Their thicker end is irregularly formed, now club-shaped, and again and more commonly elongated or bent at the point (fig. IV. *e*); they never exhibit the characteristic cork-screw spiral. The vasa deferentia of mules always remain comparatively empty, even when the testicles acquire considerable size; sometimes they are altogether wanting; in cases in which they are most largely developed, their club-shaped convoluted extremities in connexion with the cloaca, are relatively of insignificant size, and their contents consist of granules and larger globules, similar to those of the testicle, and as much as the $\frac{1}{100}$th of a line in diameter; of dimensions therefore that are never seen in other perfect birds. Proper spermatozoa, even of the insufficient size and imperfect forms of those described as occurring in the testicle, are never to be discovered in the efferent duct.

§ 13. If we now place the particulars that have been mentioned in the preceding account of spermatozoa under general points of view, the following are the conclusions that, in the present state of inquiry, may be come to:—1, spermatozoa are essential elements of the spermatic fluid, and always exist in the semen that is capable of engendering, during the whole of the limited and periodically returning season of heat among animals in general, in man and

many domestic animals during the period of their highest bodily perfection (vide § 5); 2, spermatozoa form the principal mass of the semen perfectly elaborated (§ 3); 3, spermatozoa exhibit diversities of magnitude and form that are constant, among which certain general types in relation with the several classes, orders, and families of animals are not to be overlooked, and which in numerous cases are characteristic in regard to the individual species (§ 5); 4, in one and the same species of animal, and in the same individual, no more than one determinate form of spermatozoon is ever encountered; 5, nothing like a determinate internal organization can yet be said to have been certainly discovered in any spermatozoon (§ 6); 6, the motions of the spermatozoa are extremely various, and throughout bear the character of volition (§ 7); 7, the continuance of the motions, the influence of different fluids, of temperature, and so on, vouch for an independent life in the spermatozoa, which is only dependent in a certain degree, more or less, on that of the animal in which they are found (§ 9); 8, their mode of development is cyclic, and occurs in harmony with the general laws of animal development, with especial modifications, and having certain analogies, to that, namely, of the cercaria and entozoa (§ 10); 9, as a rule, hybrids produce no genuine spermatozoa (§ 12). As a general conclusion, it may be stated, that spermatozoa are essential elements of the seminal fluid, and bear a specific relation to the generative act; they are so far comparable to the blood-globules, which present themselves in the same manner as essential typically organized constituents of the blood amid the liquor sanguinis, just as the spermatozoa present themselves amid the liquor seminis. Whether they are really animals or not cannot now be determined with absolute certainty, inasmuch as the chief criterion of animality—an internal organization, an alimentary apparatus, &c.—has not up to the present time been satisfactorily demonstrated; their independent motions and mode of development, however, speak for their animal nature. The views hitherto entertained in regard to the spermatozoa, that they are mere parasites, accidental entozoa, collateral effects of the reproductive power, &c., are unlikely and hardly tenable. But whether their formation may be most readily explained by the hypothesis of equivocal generation, or by that of parental reproduction—admitting them to be true animals—is at present doubtful [37].

37 These conclusions follow as consequences from the observations and facts adduced in the preceding paragraphs of the text. I cannot, therefore, in any way assent to the views of Burdach and Baër, according to which the formation of

§ 14. *Physical and Chemical Analysis of the Spermatic Fluid.*

The accounts we have of the physical peculiarities and chemical constitution of the spermatic fluid are for the most part either erroneous or defective, inasmuch as it has hardly yet been examined in a state of entire purity; indeed it is hardly possible to procure it without any admixture of mucus and epithelial scales[38]. In its normal state it is a thick, tenacious, whitish, grayish, or slightly yellowish coloured fluid; it is heavier than water, and forms an emulsion when shaken up with it. The peculiar odour usually described as belonging to the spermatic fluid, and which is commonly likened to that of grated bones, most probably inheres in one or other of the fluids with which it is mingled at the moment of ejaculation; the pure seminal fluid both of man and animals appears to have no decided or peculiar odour[39]. Normally the

the spermatozoa is a mere collateral effect of the reproductive power, an entozoic genesis, which occurs most abundantly in the spermatic fluid, because this among all the organic matters and secretions is endowed with the highest amount of plasticity. The decision of the question as to the mode of production of the spermatozoa, whether it is *parental* and from others like themselves, or *equivocal*, does not involve aught of peculiar interest as regards them in a physiological point of view. I allow that the late researches of Ehrenberg and of Schwann, and to theirs I may add my own, take away almost every support from the assumption of an equivocal generation in regard to any class of animals whatsoever; with regard to the Infusoria in particular, I now declare myself entirely of the opinion of Ehrenberg. All inquiry has hitherto failed to discover in what manner the entozoa originate. It seems impossible that their ova can be transported by the circulation and deposited in determinate places suitable for their evolution; the ripe ova of the smallest human entozoa are much larger than the smallest capillary vessel; the smallest ova I have observed are those of the tænia solium ($\frac{1}{80}$th of a line in diameter), of the trichocephalus dispar ($\frac{1}{50}$th of a line in diameter), and of the ascaris vermicularis ($\frac{1}{10}$th of a line in diameter), and the diameter of the finer capillaries varies from the $\frac{1}{150}$th to the $\frac{1}{300}$th of a line in diameter. Various hypotheses might be started in regard to the genesis of the spermatozoa, and supported with various reasonings; upon this subject, as also on that of equivocal generation, I refer to the *General Physiology*. (Book IV.)

[38] All existing analyses of animal substances have little value, partly because of the manner in which they are usually reported, partly because of the imperfection of the elementary analyses, and partly also, and this applies particularly to the semen, the blood, &c., because a great variety of most heterogeneous principles, which ought to be separated from one another, and reported on severally, are blended together, and the composition of all is given under one category. Microscopical analysis ought henceforth to go hand-in-hand with that which is purely chemical.

[39] I have seldom perceived any peculiar smell from pure spermatic fluid, and believe that in many cases the secretions of the vesiculæ seminales, of the prostate,

spermatic fluid shows weak alkaline reaction, and when dried and burned it exhales an ammoniacal smell; the ammonia, however, is a product of the decomposition, and is only formed at the moment this takes place. Chemical analysis shows it to consist of albumen, phosphatic and hydrochloric salts, and a peculiar animal matter called *spermatine*. No kind of crystal is ever found in fresh semen; it is only in such as has stood long that salts are formed and deposited in crystals, which on examination are usually found to consist of phosphate of lime[40].

§ 15. *Microscopic Analysis of the Ovum.*

The place of formation of the OVA, through the whole animal series, is the ovarium or female *testis*, as it used to be styled by the older writers. The OVARIA, in the vertebrata, consist of a more or less condensed cellular tissue, which not uncommonly exhibits a coarsely fibrous texture, in the interstices of which the ova, more or less crowded together, are imbedded in large round cells (fig. VIII.). This nidus, or stroma, is in general

of Cowper's glands, and of the other accessory secerning apparatus, which is often so largely developed, give rise to the peculiar odour, often of a very penetrating kind, in the horse for example, which is remarked as belonging to ejaculated semen.

[40] On the peculiar properties and chemical analysis of the spermatic fluid, see Burdach, op. cit. I. 110, Berzelius's *Elements of Animal Chemistry (Lehrb. der thierischen Chemie,* übers. von Wöhler, 1831, S. 522), and Thomson in Todd's *Cyclopædia,* II. 458. In the human spermatic fluid Vauquelin found ninety parts of water, one of soda, three of phosphate of lime, traces of muriate of lime, and six of a peculiar substance (spermatine?). These substances Lassaigne also detected in the spermatic fluid of the horse, and in addition, muriate of magnesia, and muriate of soda and of potash; Fourcroy and Vauquelin met with precisely similar elements in the sperma of fishes, and farther phosphorus. Gleichen paid particular attention to the crystals that occur in the seminal fluid, and in his work quoted above, tab. II., he has given representations of those he met with in that of the human subject.

FIG. VIII.

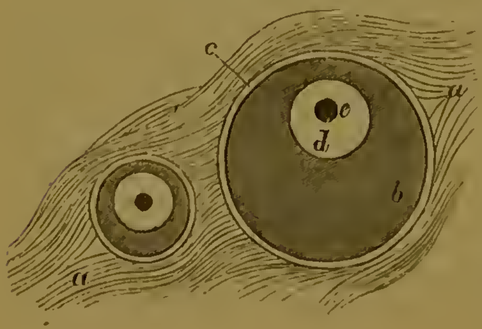

FIG. VIII.—Primary ova of the bird, magnified; scarcely to be seen by the naked eye:—*a*, stroma, or substance of the ovary, composed of thick fibres; *c*, chorion, or theca of the ovum, so thick as to be seen in the guise of a ring; *b*, yolk; *d*, germinal vesicle; *e*, germinal spot. The structure of the smaller ovum is the same.

much more delicate in the invertebrate series, and the little ovules, in closely packed masses, fill various small blind ducts, of the aggregation of which the ovaries consist. Immediately around the cell where the ovum lies, there are networks of blood-vessels, which enter the theca or capsule which includes each individual egg, and are ever the more conspicuous the larger and riper the egg is (fig. XXIV. *b*, *c*) [41].

§ 16. The OVUM still included in the ovary consists of the following essential parts, which are presented more or less conspicuously even in those of the smallest size:—1st, an external transparent tunic [chorion?], without perceptible structure, and unfurnished with blood-vessels, but very generally throughout the vertebrate series of animals connected with the ovary by a particular external lamina composed of the cellular tissue of the surrounding nidus and of blood-vessels—the capsule or theca of the ovum (fig. VIII. *c*) [42]; 2nd, of the vitellus, or vitelline globule, the proper contents of which are very generally transparent and developed in very moderate quantity in the smaller ova, but subsequently much increased by the assumption of new matter, and separated into different elements; even at a very early period there is formed around the vitellus or yolk a peculiar, exceedingly delicate membrane without perceptible structure—the vitelline membrane (fig. VIII. *b*); 3d, of a perfectly spherical transparent vesicle, sunk amidst the vitellus—the germinal vesicle—*vesicula prolifera* s. *germinativa*, which, besides a perfectly colourless fluid, contains one or more dark corpuscules, that appear as nuclei through the including membrane in the shape of opaque spots—the GERMINAL SPOT —*macula germinativa* (fig VIII. *d*, *e*) [43].

§ 17. The VITELLUS or YOLK in almost all the less forward ova

[41] For a particular account of the form and structure of the ovaria in the animal kingdom generally, see my *Elements of Comparative Anatomy (Handbuch der vergleichenden Anatomie)*, and the paragraphs that follow.

[42] To obtain conviction of the existence of this transparent structureless chorion [?], the ovary of one of the invertebrate animals—for instance the unio—should be selected. In the higher vertebrate animals this chorion [?] under the microscope presents itself as a ring of variable thickness; in ova more advanced it is found grown to the external vascular capsule, *theca*, (the later *calyx* of the ova of birds, amphibia, and fishes (fig. IX. *a*, *c*). In regard to the structure of the ova of man and the mammalia see farther on.

[43] The remarkable and prevailing similarity in the structure of the ovum through the entire series of the animal kingdom, I have made it my particular object to exhibit in my *Prodromus Historiæ Generationis*, fol. Lips. 1836. The article Ei (ovum) in Ersch and Gruber's *Encyclopædie* may also be consulted with advantage, as a commentary on what has here been said.

of the various tribes of animals is a transparent colourless fluid, in which by degrees small darker granular elements are developed. With the growth of the ovum larger vitelline globules make their appearance, which are themselves filled with smaller granules or molecules, and occasionally also with a few scattered larger and darker globules; mingled with these, variable numbers of oil or fat globules may be discovered, and in addition and everywhere interposed between the vitelline globules, the albuminous colourless fluid in small quantity, which precedes the formation of the proper elements of the yolk. The elements within the several vitelline globules undergo a gradual change as the ovum continues to advance in its development. In the centre of the yolk there is a kind of space or cell which is filled with vitelline matter of a lighter colour (fig. IX. *i*) than the rest; from this there proceeds a canal filled with the same matter towards the surface, to which the germinal vesicle, having quitted the central parts of the yolk, has now also attained, where it appears imbedded in a circular layer of the yolk of a paler yellow colour, known as the *discus proligerus, discus vitellinus s. stratum proligerum*, (fig. X. *b, b*). The globules of this discus proligerus, which are also filled with smaller globules, like the vitelline globules in general, are distinguishable under the microscope from those of the rest of the yolk, and it appears that the stratum of globules lying in immediate contact with the general vitelline membrane, forms a particular loosely connected layer [44].

[44] The description here given applies in particular to the yolk of the bird's egg, in which even the smallest ova are found already full of dark vitelline molecules, which rarely happens among other animals. The structure and arrangement of the elements of the vitellus form one of the most difficult subjects of microscopical investigation; it is one, therefore, which is by no means to be held as exhausted. It is especially difficult to conclude as to the

FIG. IX.

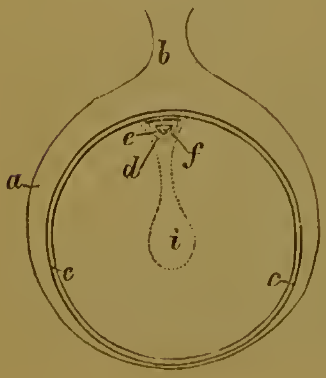

FIG. IX.—Section of a yolk almost ripe, included in its theca and calyx:—*b*, petiole or stalk connecting the calyx with the ovary: *a*, thicker substance of the calyx united with the theca of the ovum; *c*, vitellary membrane; *d*, germinal vesicle, which by and by becomes the cumulus proligerus of *Baër*, the nucleus cicatriculæ of *Pander*; *e*, proligerous disc; *i*, central cavity of the vitellus, its duct proceeding upwards.

§ 18. The GERMINAL VESICLE[45] is very large, and in relation to the whole mass highly developed in the smallest ova; it not un-

relationship between the finer molecules and the vitelline globules and their envelopes, between the oil-globules and the vitelline globules, and so on. The molecules, which exhibit lively molecular motions when the vitelline globules are burst, are partly of excessive minuteness, and appear, even out of the globules, to be suspended in vitelline matter. Baer describes the elements of the vitellus of yolk in the following terms:—"The granules, upon which the yellow colour of the substance of the yolk depends, are of different kinds. Some are larger and pretty regularly globular; they have a diameter from the 0,005th to the 0,0125th of a line, and themselves consist of still smaller less dissevered granules. In far greater numbers appear a countless multitude of granules, of such minuteness, that even under a high magnifying power they only show as points, without any distinctly determinable forms. Between these granules in point of dimensions there are others, clearer masses, the shape of which is not regularly round, but generally elongated, which, despite their clearness, observers agree in supposing not to be hollow vesicles, in which case they would also be more regular in their form. These bodies are not to be confounded with the glancing clear oil-globules which are always met with as elements of the yolk, and look much more like small pieces of albumen. There is still a fourth kind of corpuscule, of a round figure, smaller than the sort first described, and containing in its interior a small round granule or vesicle; this fourth kind of body is generally only encountered in the vicinity of the central cell." *History of the Evolution of Animals* (*Entwickelungsgeschichte der Thiere*, Bd. II. S. 19). Schwann has given very good representations of the yolk-globules or yolk-*cells*, such being his view of their constitution. Vide his Microscopical Researches on the uniformity in the structure and mode of growth of animals and vegetables (*Ueber die Einstimmung*, &c. S. 55, Berlin 1838). Schwann distinguishes between the globules of the vitelline cavity and those of the yolk in general. The former occur in the vitelline canal, and in the spot entitled nucleus cicatriculæ, or nucleus of the tread. They present themselves as perfectly round balls or globules with smooth margins, which contain in their interior a smaller globule with a sharp contour which resembles an oil-globule. The globules of the general substance of the yolk again are larger, their contents are granular, mostly without any smaller globule as a nucleus; they are extremely sensitive to the action of water. Schwann believes that, except the contents of the yolk-globules, no other finely granular substance occurs free as an element of the yolk. [On this very interesting but difficult subject, see the recent work of Reichert entitled, The Life of Evolution in the Vertebrata (*Das Entwickelungsleben im Wirbelthierreich.* Berlin, 1840.) pp. 87 et sqq.]. The synonyms of the stratum proligerum are rather numerous and confusing. Baer, too, distinguishes in it the flatter, discoidal portion under the title of *discus proligerus;* the middle portion of the same stratum, again, which is thicker, and stretches under the germinal vesicle into the yolk (fig X.), is named by Baer the *cumulus proligerus,* and by Pander the *nucleus cicatriculæ,* or *nucleus of the tread;* I have spoken of the whole formation in my Prodromus under the name of the *discus vitellinus.* Consult § 47, where the structure of this part is described in the new-laid egg.

[45] The discoverer of the germinal vesicle is Purkinje, after whom this part has also been called the vesicula Purkinji. It is fully described by him in his *Sym-*

frequently constitutes a full half of the entire ovulum. The yolk with its including membranes then surrounds it pretty tightly. This vesicle lies at first at or near the centre of the ovulum; but in the same proportion as the yolk in general advances in its growth, the vesicle is found to approach the periphery, until it is immediately under the vitelline membrane, where it lies imbedded in the middle of the disciform granular mass named *discus proligerus* s. *vitellinus,* the subsequent *stratum proligerum.* The vesicle is sunk in a depression of the vitelline disc, but extends somewhat beyond this superiorly, and tending towards the inner aspect of the vitelline membrane (fig. X. *B*); the germinal vesicle may therefore be seen even with the naked eye in middle-sized ova, in which, generally speaking, it has already attained its full development, shining through the vitelline membrane towards the middle of the vitelline disc (fig. X. *B*). It is completely spherical, but becomes flattened in many animals, frogs among the number, at a late period[46]. It consists of a simple structureless, perfectly transparent, and extremely thin membrane, which, however, is not

bolæ ad ovi avium historiam ante incubationem, 4to. Lips. 1830, and figured in his first plate. See the comprehensive article Ei by the same writer in the *Encyclopædisches Wörterbuch,* B. X. S. 107 (1834). Representations of the germinal vesicle and macula in ova at an early period will be found in my *Prodromus,* and article Ei in Ersch and Gruber's Encyclopædia.

[46] The bedding of the germinal vesicle in a pore or depression of the *discus vitellinus* or proligerous disc, and its appearance through the vitelline membrane, are particularly conspicuous in birds, lizards, and serpents; in the riper ova of the frog the germinal vesicle appears as a relatively large flattened body, under the black vitelline or proligerous disc; to obtain a view of it, an ovulum must be opened with fine scissors, when it will generally be found to escape and become perfectly visible to the naked eye. A perpendicular section through ova that have been hardened for a short time in acetic acid, exhibits the relative positions of the parts very plainly. See my *Contributions to the History of Generation, &c.* (Beiträge tab. II. fig. 6.) The relations are similar in the salamander.

Fig. X.

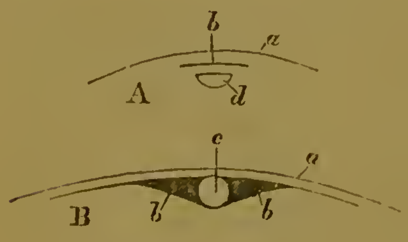

Fig. X.—*A*, ideal section of part of the yolk of a hen's egg expelled from the oviduct; *a*, vitelline membrane; *b*, germ (blastos); *d*, cumulus proligerus: these parts are represented as more remote from one another than they are in nature. *B*, ideal section of part of the yolk before its separation from the ovary; *a*, vitelline membrane; *b*, *b*, discus proligerus; *c*, germinal vesicle.

without some degree of elasticity, and a power to resist pressure that is not too violent. It is completely, and even tightly distended with a perfectly colourless and limpid fluid, the albuminous nature of which is proclaimed by its coagulating in alcohol and acids.

Besides what has now been described, in man, the mammalia, birds, the scaly amphibia, and many invertebrate animals, an opaque spot is observed upon a particular part of the germinal vesicle; this is the MACULA GERMINATIVA, the germinal spot (fig. VIII. *e*, fig. XI. *d*, figs. XV and XVI. *g*). Attentively studied, the germinal spot, even in the smallest ova, in which indeed it is often most conspicuous, presents itself as a rounded, granular formation, attached to the inner wall of the membrane of the germinal vesicle[47]. It happens not unfrequently that amidst the finely granular tissue of which the germinal spot consists, a few larger molecules may be distinguished; occasionally it has even the appearance as if it were surrounded by a delicate and closely-applied covering or capsule[48]. Under pressure, or when rolled about, the germinal vesicle assumes different forms[49]. In many animals, as for instance in naked amphibia,

[47] To gain a general idea of the structure of an ovarian ovum, one of the invertebrate animals—an anodonta, or, still better, an unio—should be chosen. Here there is no difficulty in distinguishing an outer coat, *membrana externa* s. *chorion* [?], surrounding, at a greater or less distance, the vitellus or yolk, which is to be understood as included in its own peculiar covering, the *membrana vitellina*; the vitellus will be observed including an extremely beautiful, pellucid, and large germinal vesicle, whose figure-of-eight formed germinal macula is particularly distinct. Vide my *Prodromus*, tab. I. fig. 5. In the ova of the spider and snail, the structure is also very distinct.

[48] The germinal macula appears in many animals to be surrounded by a particular covering, a circumstance which I have often remarked in spiders, but which I have seen with unusual plainness in julus.

[49] I have succeeded in pressing the germinal macula as a pulpy or semi-consistent body into different shapes, with more than usual ease, in the ova of lepidoptera. Vide *Prodromus*, tab. II. fig. 22.

FIG. XI.

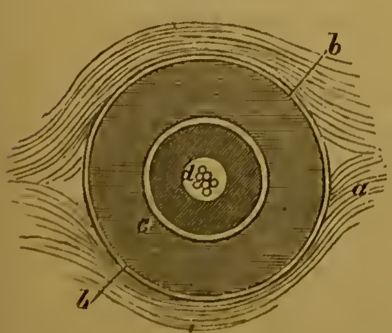

FIG. XI.—Section of an immature ovum of the rabbit, which may be compared with fig. VIII; *a*, *a*, stroma; *b*, *b*, Graafian vesicle, in its centre the ovulum *c*, and in the centre of this again the germinal vesicle *d*, in which the germinal spot, constituted by a congeries of granules, is situated.

the bony fishes, and several of the invertebrate series, a considerable number, often as many as from eight to ten dark round maculæ may be seen in the germinal vesicle of even the smallest ova, as the optical expression of certain small globular-shaped formations, attached to the inner aspect of the paries of the vesicle through its whole extent. These maculæ are of a somewhat more sluggish or oleaginous consistency than the germinal macula itself in other cases, and it frequently enough occurs that among them one larger, more opaque, and granular-looking body can be distinguished, which perhaps were correctly viewed as the true macula germinativa[50]. Even in those cases where the germinal macula never occurs save singly, numbers of new granulations in the shape of small dispersed globules may be occasionally observed in the smaller ova, and almost invariably in those that are farther advanced, produced upon the inner wall of the germinal vesicle, by the growth of which the originally larger, more conspicuous, and more opaque germinal macula is rendered indistinct or totally obscured[51].

§ 19. It is extremely difficult to speak decidedly with regard to the successive formation of the several elements of the ovum, as these are described in the preceding paragraphs. A general comparison of the formation of ova in the animal kingdom, shows that the germinal vesicle and macula are the parts which soonest attain their complete development; in insects it even seems that in the first instance these two elements only are produced, and that the vitellus or yolk is deposited around them at a subsequent period. In general, too, the external velamina or covering—the chorion or general envelope of the ovum, and the vitellary membrane or special envelope of the yolk—are encountered at a very early period, as also a very small quantity of vitellary matter; but the germinal vesicle still forms the principal part of the ovum[52]. Occasionally

[50] To observe this formation as it appears of numerous rounded germinal maculæ, let the ovary of a frog or fish, or cray-fish, be chosen. Vide *Prodromus*, fig. xvi, xxv, and xxvi. In the trout, and others of the salmonidæ, I have frequently discovered a larger macula, or body of a different appearance, which was perhaps the proper germinal macula.

[51] Examples of this will be found in the *Prodromus*, fig. xxiv. and xxvii.

[52] Examples of this kind, in which the yolk is still very slightly developed, and the germinal vesicle composes the principal part of the ovum, may be seen in my *Prodromus*, in the asterias, for instance (fig. III.); and, again, in insects, fishes, and even frogs. The successive development of the several parts of the ovum can be very advantageously studied in the tubular ovaria of insects; in the agrion, for example, tab. II. fig. 1, of my *Beiträge*. Still, even in the smallest of these ova, the vitellus or vitellary vesicle is to be distinguished as a cover-

it seems as if even in the ovary there were a small quantity of albumen formed between the chorion [?] and vitellary membrane, namely, at that point where the chorion with the whole ovum is about to pass from the ovary into the oviduct, uterus, or particular receptacle of the ova [53]. In those cases, however, in which the chorion [?], as in the ovipositing vertebrata, is connected with the outer capsule formed of the stroma or substance of the ovary, and remains behind under the name of the calyx, after the escape of the ovum, the albumen is always secreted subsequently in the oviduct, in the course of which it accumulates around and includes the vitellus [54]. The germinal vesicle may be viewed as a cell—as the primary cell—of which the germinal spot forms the nucleus; so that it would perhaps be well to style the germinal spot the germinal nucleus—*nucleus germinativus*. This nucleus disappears when new granulations are evolved in the contents of the cell (the fluid of the germinal vesicle). The primary cell lies within another cell, the vitellary cell, the contents of which in their turn become filled with new cells—the vitellary globules. The outermost cell, in which both of these principal cells are included, would then be the chorion [?] and the ovarian capsule or theca [55].

ing or envelope to the germinal vesicle. Whether the annular formations having a nucleus in their interior, which lie one behind another in the fine capillary terminations of the ovaria, are to be considered as germinal vesicles, or not, is a question still undecided. See the account of these in the proper place. [It may here be mentioned, that the observations of Dr. Martin Barry confirm the opinion that the germinal vesicle is the primitive portion of the ovum. The conclusions of this able observer will be mentioned further on. Vide his *Researches in Embryology*, Phil. Trans. 1838, p. 308. R. B. T.]

[53] This at least appears to be the case in the mytilacea: if the ova of these animals be put into water, a space of greater or less extent is discovered between the vitellus and the chorion [?], which is perhaps occupied with albumen. Vide *Prodromus*, fig. V.

[54] The formation of the albumen in the oviduct is very easily followed in the class of birds, and will be spoken of more fully in our history of the development of the embryo.

[55] The highly ingenious views and masterly researches of Schwann, led to the above attempt to explain the different parts of the ovum, of the germinal vesicle in particular. Schwann believes that the same law must be admitted in regard to the elementary form of the animal tissues, as that which Schleiden pointed out as obtaining among vegetables. Every formation consists of cells, which have excentric nuclei, which may subsequently disappear, an event that especially happens when new cellular elements are evolved in their vicinity. The nucleus, or that which is regarded as the nucleus, is often found itself to inclose nuclear corpuscules in its interior. The membrane of these cells is often difficult to be distinguished; for example, when it is extremely thin, when the nucleus lies very

§ 20. The ovum in man and the mammalia exhibits the same general elementary structure as in other lower animals, yet with such modifications as make a separate account of it indispensable. The most remarkable peculiarity in man and the mammalia is the extraordinary minuteness even of those ova that are farthest advanced, a circumstance which depends on the very small quantity of vitellus entering into their constitution. The ripest ovum in the ovary of the human subject, and of the mammalia, generally measures no more than from the fifteenth to the twentieth part of a line in diameter; it happens very rarely indeed that they are seen so much as the tenth of a line in diameter; so that they are only to be distinguished with extreme difficulty with the naked eye; this is the reason why they were so long overlooked, or mistaken, and why it is only in very recent times that they have been studied with reference to their intimate and more delicate structure[56].

close, and so forth. In the majority of cells the nucleus is absorbed at a later period; it is only in a few that it remains as a permanent formation; in the interior of older cells younger ones are very commonly evolved. In the application of this law to the particular case of the germinal vesicle, Schwann proposes many questions, and expresses himself as in doubt whether to consider the germinal vesicle as a young cell, and the germinal macula as its nucleus, or to view the whole germinal vesicle as the nucleus of the vitelline cell. Vide Schwann, *On the Uniformity in the Structure and Mode of Growth among Animals and Vegetables*, p. 50. That the germinal vesicle is no proper nucleus, I think probable on many grounds: frequently it appears that the germinal spot, as germinal nucleus, actually contains small nucleoli. Vide *Prodromus Hist. Generat.* tab. II. fig. 30, *b*.

[56] The true discoverer of the primary ovum of mammalia is von Baer: *Epistola de Ovi Mammalium et Hominis Genesi*, 4to. Lips. 1827. It seems probable, however, that De Graaf and Prevost and Dumas had seen it previously. Von Baer was not acquainted, at the time he wrote his Epistola, with the more delicate and true structure of the ovum; he in fact assimilated the whole ovum of mammalia to the germinal vesicle of birds, &c. and mistook the granular layer of the Graafian vesicle for the vitelline or proligerous disc. [Purkinje, however, the discoverer of the germinal vesicle, expressed his doubts of the correctness of this opinion of Baer, and stated his belief that the ovulum of Baer was analogous to the yolk with its contents.—Art. Ei in *Berliner Wörterbuch*. R. B. T.] A great advance was made when the germinal vesicle was discovered in the ovum of the mammiferous animal, the fact of its existence being announced almost simultaneously by Coste (*Recherches sur la Génération des Mammifères*, 4to, Paris, 1834), and Bernhardt with the co-operation of Valentin (*Symbolæ ad Ovi Mammalium ante prægnationem*, 4to, Vratislav. 1834). The work of Bernhardt and Valentin contains at once the first accurate account and faithful representation of the structure. I was myself the first to discover the germinal macula; I also described and figured the whole ovum in its successive stages with greater care and sequence than had yet been done. Vide my *Prodromus*, and *Beiträge*, where an historical account of all the discoveries connected with the ovum of mammalia

Another remarkable peculiarity consists in the manner in which the ova are contained in the ovaria; instead of being in immediate contact, by means of their chorion, or outer envelope, with the ovarian nidus, as in other animals, they are here found included in other larger rounded cells, the GRAAFIAN VESICLES or FOLLICLES. These cells, one or more lines in diameter, lie like the capsules in the stroma or nidus of the ovaries, and glisten through the peritoneal covering of these bodies; they also not unfrequently rise above the general level of the ovary, and form globular elevations upon its surface, as is seen in the representation of the ovary of the common sow (fig. XII. *c*, *c*, *c*). If the stroma is extremely delicate or scanty, the Graafian follicles even appear as pediculated globules, a structure which occurs in the common mole, and in a still greater degree in the ornithorhynchus (fig. XIII. *a*, *a*), where the ovary comes to assume a strong resemblance to that of birds [57]. The

is given. See also the account in Valentin's *Handbuch der Entwickelungsgeschichte*, S. 9. and the observations of Krause in Müller's *Archiv für* 1837, S. 36. [The dates of the observations by which the existence of the germinal vesicle in the ovum of the mammifera was determined, are these:—Coste, *Recherches, &c.* Paris, 1834; Bernhardt and Valentin, *Symbolæ, &c.*, Vratislav. 1834. Wagner, *Einige Bemerkungen über das Keimbläschen*, in Müller's *Archiv*, 1835, (sent in 1834); T. W. Jones, ON THE OVA OF MAN, &c.; paper read before Royal Society 1835; Observations made Sept. 1834; printed abridged in Abstract of proceedings for the year, and in full, in Lond. Med. Gazette, 1838. R. B. T.]

[57] The ovum of the human subject differs in no respect from that of the mammalia generally. Vide *Prodromus*, fig. xxxiii. It rarely happens that we have

FIG. XII.

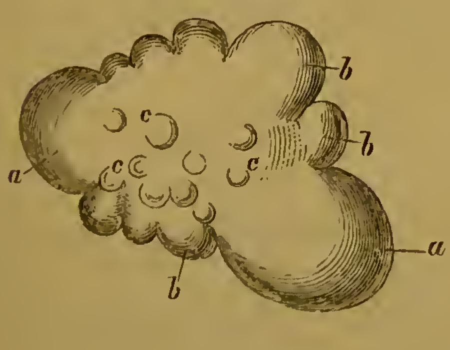

Fig. XII.—Ovarium of the sow, with corpora lutea of recent and older date: *a*, *a*, large reddish-purple coloured corpora lutea, about eight days after the bursting of the Graafian follicle; *b*, *b*, corpora lutea of later date; *c*, *c*, prominent mature Graafian vesicles.

FIG. XIII.

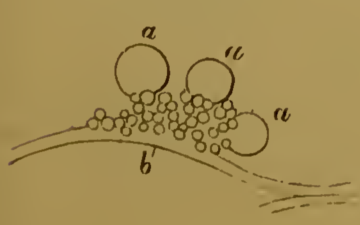

Fig. XIII.—Ovarium of the *ornithorhynchus paradoxus*, after Owen (*Philos. Trans.* 1834, pl. xxv.): *a*, *a*, *a*, three Graafian vesicles much enlarged, in consequence of impregnation; *b*, smaller unimpregnated Graafian vesicles.

Graafian vesicles consist of a double membrane, the outermost of which is extremely vascular, whilst the inner layer is velvety in appearance, from being endued with an epithelial covering. The internal space or cavity of the vesicles is very far from being filled by the ova, which are relatively much smaller; they contain, in addition, a whitish, or yellowish, thick, albuminous mass, which under the microscope appears to consist mainly of minute granules, from the 200th to the 300th of a line in diameter. These granules are generally connected by means of a tenacious fluid; they are particularly coherent in the precincts of the ovum, which is in fact imbedded in a discoidal condensed mass of these granules, precisely as the germinal vesicle is imbedded in birds and other still lower animals in the germinal or vitelline disc (fig. XV. *d, d.* figs. LXII. and LXIII. *a*). This granular disc continues attached in a greater or less degree to the ovum, when it is removed from the Graafian vesicle

an opportunity of examining a human body in so recent a state as to admit of the germinal vesicle being seen. Among the Mammalia, the cat, dog, and rabbit, are the best subjects for commencing observations upon. The Ruminantia are not so good. In the bitch the yellowish ovum may be seen shining through the peritoneal covering of the ovary and the thin membrane of the Graafian vesicle.

Fig. XIV.

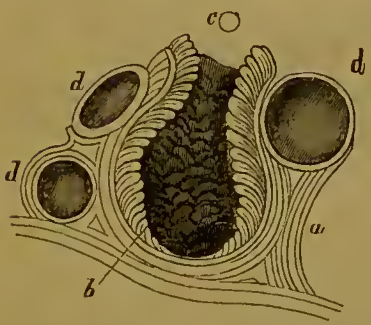

Fig. XIV.—Portion of the ovary of the *ornithorhynchus* magnified, after Owen (*Philos. Trans.* 1834. pl. xxv.) : *a*, stroma of the ovary; *b*, a Graafian vesicle which has burst, and suffered its ovum (*c*) to escape (this Graafian vesicle is in the course of change into a corpus luteum); *d, d, d,* sections of entire Graafian vesicles.

Fig. XV.

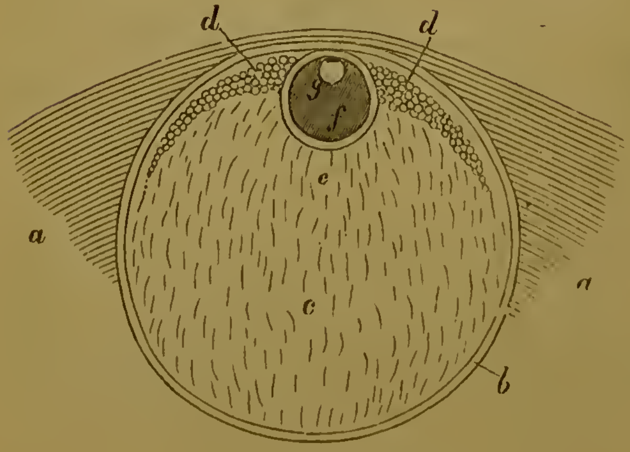

Fig. XV.—Ideal section of a ripe ovum of a mammal (the rabbit) *in situ* in the ovary: *a, a,* stroma or substance of the ovary; *b*, double tunic of the Graafian follicle; *c*, its contents, which at *d, d,* form a granular disc, in which the ovulum, *e*, is embedded; *f*, yolk; *g*, germinal vesicle with the germinal macula.

(fig. XVI. *a, a;* and figs. LXII. and LXIII. *a*), but the irregular and torn edges show that the appearance presented is due to violence; and, in fact, it would seem that this disc is continued as a membraniform granular layer under the inner membrane, so as to form a sort of loose, easily-rent capsule or covering to the other contents of the follicle [58]. The granules present a finely granular appearance, and are decomposed, but not very distinctly, on the addition of acetic acid to them, into a transparent envelope and a darker nucleus (fig. LXIII. *B. b*). In quite ripe ova (fig. LXIII. *A* and *B*) these granules may be observed as distinctly oval cells, distended with very minute molecules, and united into a membrane. If we examine this granular membrane in the bitch for instance, in ova that have begun to enlarge after impregnation, but that have not yet escaped from the Graafian follicles (fig. LXIII, *B*), the cells appear with exceedingly delicate parietes and clear nuclei, extremely like the pigmentary cells of the choroid coat of the eye. Between the granules we observe a variable number of pretty clear spaces, which are obviously due to little globules of a very pale-coloured fat or oil (fig. XVI. *b, b, b*). When still very small and immature, the ovum lies in the middle of the follicle (fig. XI. *c*); when fully formed, on the other hand, it lies immediately under the inner coat of the follicle, imbedded in its granular disc (fig. XV. *e*). To study

[58] I was long in doubt whether such an external membraniform granular layer existed or not; it was not until after Bischoff had declared his opinion in favour of its existence that I satisfied myself of its presence. Baer describes this granular layer in the second volume of his *Entwickelungsgeschichte,* p. 179, under the name of the *Körnerhaut,—membrana granulosa.*

Fig. XVI.

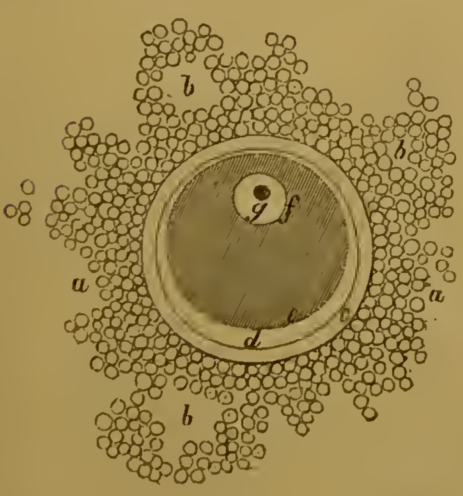

Fig. XVI.—Ripe ovum of the Rabbit, taken from the Graafian vesicle, surrounded by its proligerous disc *a, a,* the edges of which are ragged and irregularly notched; the clear parts, *b,* occurring among the granules, are pale oil globules; *c,* the thick chorion [?], or *zona pellucida,* surrounding the vitellus, *e.* The yolk, *e,* in this instance, is seen distinctly separated from the zona, and surrounded by a membrana propria, or perhaps an outer superficial layer of granules (the vitelline membrane? germ?); *f,* germinal vesicle; *g,* germinal spot. Vide figs. LXII. and LXIII.

the minute structure and the several parts of the ovum more particularly, a magnifying power of between three and four hundred diameters must be employed, under which, with the aid of gentle, not violent pressure, the entire structure becomes visible. The ovum is, in the first place, surrounded by a thick white ring (fig. XVI. *c*, and fig. LXII. and LXIII. *b*), which internally and externally is bounded by a simple, dark outline. This ring, by some entitled *zona pellucida*, by others regarded as a space filled with albumen [59], appears to be really nothing more than the optical expression of a thick external membrane—of the CHORION [?], in a word; it is highly dilatable, so that the clear ring it presents, appears thicker or thinner, in the same ovum, as the pressure made upon it is lessened or increased; it is perfectly transparent, and shows no trace of structure. Normally, the yolk or vitelline globule is in immediate contact with the chorion [?], but in very ripe ova it occasionally though rarely happens, that a space may be distinctly seen between the inner aspect of the chorion and the outer surface of the yolk (fig. XVI. *d*), which enlarges a little by the imbibition of water. Here, then, it is also obvious that the vitellus is bounded by a peculiar covering, a *tunica propria*, which appears to be a membraniform, external granular layer (the analogue of the *stratum proligerum* of the bird's egg? of the proper vitellary membrane?) [60].

The vitellus consists of a finely granular mass, amid which large globules, and, in thoroughly ripe ova, small clear globules of oil are scattered. The superficial layer of the vitellus appears to consist of granules larger in size and more closely compacted or united than elsewhere. Internally, that is, around the germinal vesicle, perhaps also in the centre, the vitellus is a clear albuminous-looking fluid almost devoid of granules (fig. LXII. immediately around the germinal vesicle) [61].

59 Valentin and Bernhardt call this ring *spatium pellucidum s. zona pellucida*. Despite the positive statement of that excellent anatomist Krause (Müller's *Archiv*, 1837), that the zona pellucida is a stratum of albuminous fluid included in a distinct delicate membrane, I am obliged to say that I cannot agree with this view, supported as it is by the authority of Schwann; the rather as I find that Bischoff, who has taken great pains with this subject, entertains the same opinion as myself. In ova that have been burst, I can always trace the rent traversing it (fig. LXIII. *c*.).

60 The space, and this is very different in different cases, between the vitellus and the chorion, is perhaps filled up by a very thin stratum of albumen. By and by, in our history of Development, this point will be investigated.

61 This clear fluid, surrounding the germinal vesicle immediately, is distinctly

The germinal vesicle (figs. XVI. *f*; XVII. *g*; LXIII. *d*) usually appears as a clear ring, and in ripe ova lies immediately under the vitelline membrane [?] and inner wall of the chorion [?]. With a little dexterity the ovum may be burst, and the germinal vesiele forced out uninjured (fig. LXIII. *d*); it is uniformly of very small size; measuring in man and the mammalia at the most the $\frac{1}{60}$th of a line in diameter. With attentive observation the dark germinal spot is readily to be distinguished amid the clear eontents of the vesicle attached to its paries, (fig. XVI. *g*, fig. LXII. and LXIII. *e*). The germinal macula is almost always seen as a simple rounded body from the $\frac{1}{200}$th to the $\frac{1}{300}$th of a line in diameter; it is very rarely observed double, or as an aggregate of granules, which, however, is sometimes the case in immature ova (fig XI. *d*). A striking difference between the disposition of the germinal vesicle in the ovum of the mammalia and that of all the other animals whatsoever, is the absenee in them of a proligerous dise—diseus proligerus s. vitellinus, in whieh, through the whole of the inferior series, it is invariably imbedded; the most eareful observation shows no sueh strueture, and no sueh relation here; and yet it is possible, and on analogical grounds even probable, that this diseoidal accumulation of granules is not aetually wanting in the ovum of man and the mammalia; perhaps the granular membrane deseribed above, which surrounds or incloses the vitellus, generally, is the analogue of the proligerous disc [62].

It is a task of great difficulty to learn any thing of the genesis or primary production of the ovum, and to follow it through its different stages of development in man and the mammiferous animals: in very young animals, even in the embryo as it approaches maturity, we can diseover ova in the ovaria, furnished with a germinal vesiele as they are at any other subsequent period of life; the vitellus is indeed much smaller, and so is the Graafian

represented in fig. LXIII; it is difficult to say whether, as in the bird's egg, it fills the central cavity of the vitellus, and is here only found in the vicinity of the germinal vesicle in consequence of the compression of the ovum.

[62] Particular care ought in future researches to be taken with a view to settle this question of the presence or absence of a germinal or vitelline disc. To me it seems highly improbable that such a relationship should actually be wanting, although the most sustained observation has hitherto shown me nothing. Connected with this, there is also the question whether or not that delicate membrane situated within the chorion [?] and bounding the vitellus, is a proper vitellary membrane, or a *stratum proligerum* surrounding the whole vitellus, in which only a certain thickening at a particular place is absent (the discus proligerus and cumulus proligerus). [See the bracketed portion of annot. 63, p. 53, signed R. W.]

vesicle, the contents of which appear to consist of larger cells, and occupy much less space than in ripe ova. (fig. XI.) The ovum with all its essential elements, however, is there, and in existence at the period of birth; very different, therefore, from the spermatic fluid, which is first eliminated possessed of its distinctive characters at the time of sexual maturity; the principal difference between a ripe and an unripe ovum lies in the greater and more especial development of the vitellus in the former[63].

[63] Embryos at the full time, or the young of some small animal, as of the mouse or rat, should be chosen for this inquiry. Carus has given a description and figure of the completely developed ovum in new-born female children (Müller's *Archiv*, 1837, p. 440, and *Ann. des Sciences Nat.* tom. vii. 1837, p. 297). [The extensive and minute researches of Dr. Martin Barry on the unimpregnated ovum require particular mention here. Dr. Barry confirms the description of previous observers as to the bilaminate structure of the Graafian vesicle. He defines this vesicle to be *an ovisac that has acquired a covering proper to itself*. The ovisac is therefore the first portion of the Graafian vesicle formed, and constitutes the internal layer of that vesicle. The formation of the ovisac, however, is subsequent to that of the germinal vesicle, which Dr. Barry, in accordance with Purkinje, Baer, and Wagner, regards as the most primitive portion of the ovum.

The early structure of the ovisac in mammalia may be seen, as Dr. Barry states, either in very young animals or in those that have lately reached maturity, when this vesicle and its contents are in the full vigour of formation. Dr. Barry finds it in young animals by placing under the microscope thin slices cut from the surface of the ovary, or, in animals after puberty, the outer portion of a large Graafian vesicle. Moderate compression is required, but it should be applied very gradually.

The first step in the formation of the ovarian ovum consists in the appearance of the germinal vesicle, which is sometimes nearly globular, at others elliptical, the long diameter then varying from the $\frac{1}{150}$th to the $\frac{1}{50}$th of a Paris line. This difference of diameter is probably owing to difference of age in the vesicles, which doubtless increase in size after their formation. The germinal vesicle at this period has an envelope consisting of certain granules of a peculiar appearance, which Dr. Barry describes as being elliptical or ellipsoidal, sometimes nearly round, and generally flattened. When lying close together, their form becomes by pressure polyhedrous. They are exceedingly transparent, yet often punctate, which latter appearance seems sometimes to arise from the presence of very minute oil-like globules. They present, with more or less distinctness, a nucleus, and two nuclei have been met with in a single granule. In the substance of the nucleus there is observable a point still darker. These peculiar granules sometimes disappear, apparently by liquefaction; preparatory to which change Dr. Barry states that he has observed them to become more spherical and brightly pellucid, seeming to contain a fluid in their interior. In size they vary from about the $\frac{1}{400}$th to the $\frac{1}{100}$th of a Paris line ($\frac{1}{4300}$th to $\frac{1}{1125}$th of an English inch), but they are often about the $\frac{1}{200}$th of a Paris line in length. As viewed by reflected light, they appear greyish white in colour; water dissolves them.

Around the germinal vesicle, then, enveloped by these peculiar granules,

§ 21. *Physical and Chemical Analysis of the Ovum.*

The yolk or vitellus, the principal mass of the ovum, is a thick, sluggishly fluent, oily-looking mass, having a certain odour, often

among which are found some oil-like globules, a membrane is soon formed, which is the *ovisac;* so that the ovarian ovum, examined in this stage, consists of an ovisac containing a pellucid fluid, in which is a large quantity of the peculiar granules described, a varying quantity of oil-like globules, and among these, and more or less concealed by them, the germinal vesicle. The oil-like globules with a pellucid fluid accumulate around the germinal vesicle, between it and the peculiar granules, and thus the formation of the yolk is indicated; this new-formed yolk becomes surrounded by two membranes, one of which is the proper membrane of the yolk *(membrana vitelli)* [?], and the other, more external, is the true *chorion* [?] (fig. XVII). Subsequently, a covering or tunic, consisting of a kind of dense cellular tissue, susceptible of becoming highly vascular, and closely connected with the surrounding stroma, is gradually formed upon the outer surface of the ovisac, and it is from the union of this membrane with the ovisac that the *Graafian vesicle* results; the "couche interne" of which, as described by Baer, is the originally independent ovisac, while the "couche externe" of that author is the covering or tunic of the ovisac just described (Baer, *Lettre sur la formation de l'Œuf*, in *Breschet. Repertorium*, 1829).

The analogy between the ovarian capsule that contains the yolk in the bird and the Graafian vesicle has been long acknowledged; it was particularly indicated by T. W. Jones; and according to Dr. Barry, the ovarian calyx of birds, if deprived of its peritoneal investment, and what there is of the parenchyma of the ovary, would present a structure analogous to the Graafian vesicle of mammalia. The ovarian ovum of birds in fact passes through precisely the same stages of formation as that of the mammalia.

In reptiles and fishes the same formations are observed, and in the same order, with the exception that the fluid of the ovisac does not generally present the peculiar granules described as occurring in mammalia and birds.

The situation of the ovum in the early period of its formation is in or near the centre of the Graafian vesicle, where it is completed in all its parts, though

FIG. XVII.

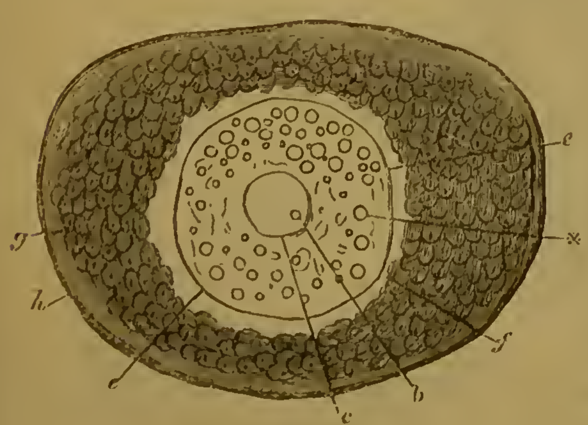

FIG. XVII.—Ovum of the cat, magnified, after Barry:—*b*, germinal spot; *c*, germinal vesicle; *, oil-like globules in the yolk, which consists besides of a pellucid fluid and minute granules; *e*, membrana vitelli [?] almost concealed by the chorion [?] *g*, peculiar granules; *h*, ovisac. [The peculiar granules, Schwann and Dr. Barry have since found to be nucleated cells. R. W.]

decided enough, but with nothing distinctly specific about it. The colour of the yolk is most usually yellow, but the shade varies

probably not matured. In this situation it appears to be supported by an equable diffusion of the peculiar granules of the ovisac throughout the fluid of the vesicle; subsequently, however, the peculiar granules become aggregated together in certain parts, leaving spaces occupied by fluid, and at length arrange themselves so as to constitute three distinct structures:—namely, 1. The *tunica granulosa*, formed by some of the granules being collected on the surface of the chorion or outer investing membrane of the ovum. These granules have been hitherto regarded as a portion of the "proligerous disc" of Baër which adheres to the ovum, and escapes with it from the Graafian vesicle. But Dr. Barry finds on attentive examination that those granules which immediately surround the ovum are in a state of denser aggregation than the rest, invest the whole surface of the ovum, and form a distinct tunic (to which he gives the name *tunica granulosa)*, perfectly spherical in form, and which he has sometimes succeeded in obtaining freed from the other granules which adherent to it escape from the Graafian vesicle. 2. The separation of the granules of the ovisac forms a layer, collected on the inner surface of the ovisac, and constituting the *membrana granulosa* of Baër. And, 3. Between the two structures just described, a third is formed, which Dr. Barry describes as "an assemblage of structures, consisting of a central mass, in which the ovum (in its granular tunic) is contained, and of cords extending from the membrana granulosa to the central mass. These structures had not been previously described, and Dr. Barry, attributing to them the office of suspending the ovum and retaining it in its situation in the fluid of the Graafian vesicle, has named them the *retinacula*. They are seen indistinctly in most animals, but may be best observed in the rabbit; their arrangement will be clearly understood by referring to the accompanying figures (figs. XVIII. and XIX.)

The office of the retinacula appears to be not only to suspend the ovum in the

Fig. XVIII.

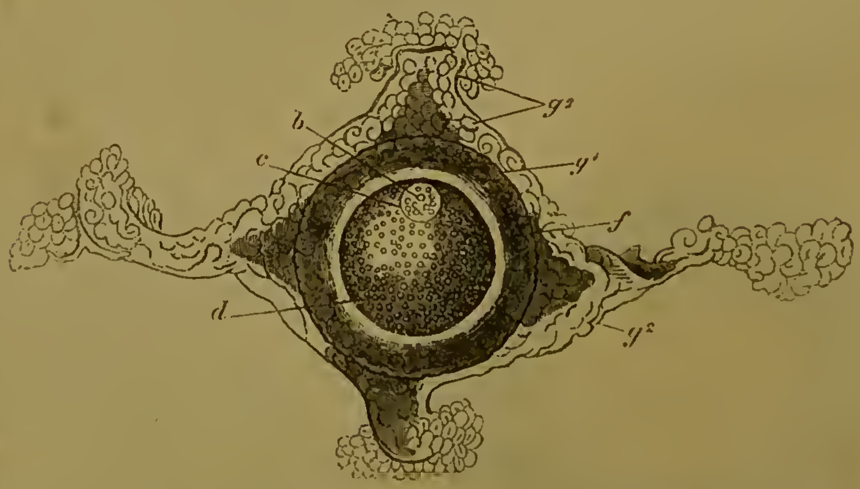

Fig. XVIII.—Ovum of the rabbit, magnified 240 diameters (after Barry). The retinacula with their membrane removed from the Graafian vesicle:—*b*, germinal spot; *c*, germinal vesicle; *d*, yolk; *f*, chorion [?]; g^1, tunica granulosa, with four tail-like processes prolonged into g^2, the retinacula.

greatly, tending more or less on the one hand to red, on the other to white; it is very commonly of a pale yellow or whitish in the

fluid of the Graafian vesicle, but to convey it from the centre, where it is at first formed, to the periphery of that vesicle, and to retain it there. This seems evident from the fact that, as the ovum approaches the periphery of the Graafian vesicle, the granulous cords become shortened on one side of the central mass, while those on the other disappear. When the ovum has reached the surface of the vesicle, the central mass in which it is contained has become smaller, and in many instances nearly of the size and form of the tunica granulosa; sometimes the band-like portions of the retinacula become reduced to four in number, and sometimes only two remain; they often seem closely pressed against the inner membrane of the Graafian vesicle. The following is the order of formation as to time of the more prominent parts of the ovum and Graafian vesicle in mammalia:—1. The germinal vesicle, with its contents. 2. An envelope, consisting of peculiar granules and oil-like globules. 3. The ovisac, which forms around this envelope. 4. The yolk, which forms within the ovisac around the germinal vesicle. 5. The proper membrane of the yolk [?], which makes its appearance while the yolk is still in an incipient state. 6. The chorion [?]. 7. The proper covering or tunic of the ovisac, the tunica granulosa, the retinacula, and the membrana granulosa. M. Barry, *Researches, &c.* pt. i. *Phil. Trans.* 1838. R. B. T.

In the preceding paragraph and the long annotation 63, the reader will have observed that the words chorion and vitelline membrane, as often as they occur, have bracketed points of interrogation placed after them, thus [?]. For more particular explanation of this, see the addition to annot. 137. Here it is indispensable to say that observers differ as to the time and mode of formation of the undoubted chorion. Some with the author, Bischoff, Dr. Barry (in his first series) &c., maintaining that the chorion exists as an original element of the ovarian ovum, its representative there, being the thick transparent membrane, or zona pellucida; whilst others, Coste, T. Wharton Jones, &c., declare that what is spoken of by Wagner, Bischoff, and Dr. Barry, as the *vitellary membrane* in the ovum of the mammal is a thing of idea and inference only, nowise demonstrable; that the peripheral globules of the ovum cohere by a vital or mechanical attraction, or at most a kind of agglutination, and are not held together in consequence of being surrounded by any membrana propria; that the zona pellucida of the mammal's ovum, as the first consistent tissue which surrounds the yolk,

FIG. XIX.

FIG. XIX.—Graafian vesicle and ovum of the rabbit, magnified 100 diameters (after Barry), to show the separation of the peculiar granules of the ovisac into three incipient structures:—g^1, tunica granulosa; g^2, the retinacula; g^3, membrana granulosa.

mammalia, amphibia, and fishes; and in many birds it is of a bright yellow, and even approaches a red: it is only among invertebrate animals that other colours, such as green, violet, blue, bright red, and flame colour are encountered; these are all, but rarely, met with, as are also brown and dark green, which, however, occur in a few instances[64]. The seat of the colour of the yolk is in the vitelline globules, not uncommonly also in the oil-globules, which are often plentifully mingled with the proper vitelline globules; in some cases the vitelline are of a very different colour from the oil-globules of the yolk[65]. The principal constituents of the yolk are water, albumen, and oil; the oil yields a crystallizable fat, which appears

ought to be regarded as the true vitellary membrane; that this zona pellucida of the ovum of the mammiferous animal is in fact the analogue of the vitelline membrane of the ovum of the bird. T. Wharton Jones was the first who saw that after impregnation in the mammal, a new structure, which he regards as the future and true chorion, is added to the ovum, even before it quits the ovary, and that the old vitellary investment, the thick transparent membrane or zona pellucida (chorion of Wagner) by and by disappears, the yolk having now the new structure for its sole membranous investment. R. W.]

[64] In many birds, the corvidæ, many palmipeds, &c. the yolk is of a very bright or reddish yellow colour; in other birds, again, it is of a pale yellow, as in the common fowl. The yolk is not very uncommonly green in insects: for example, in many butterflies it is of a beautiful grass green; so is it also among annelida in clepsine, and among crustacea in many species of cypris. It is red, according to Grant, in lobularia digitata; brick-red, according to Carus, in unio litoralis. I have found it flame-red in hydrachna histrionica, pale violet in many spiders, dark violet-blue in gammarus pulex, azure-blue in anatifa lævis; it is very frequently orange-coloured or sulphur-coloured, as in unio pictorum; milk-white, as in cyanea Lamarkii; the superficial vitelline or proligerous layer is of a blackish green in the ranidæ. There appears to be no law in regard to the colour of the vitellus in the lower classes of animals; it is frequently of the most opposite and dissimilar hues in the most closely allied genera.

[65] When the oily element of the yolk collects into distinct large drops, these may be seen, even externally, in transparent ova; the oil-globules always refract the light strongly, and are often of a colour different from the rest of the yolk. In the salmo thymallus, for example, the yolk is clear and whitish, but there is often an accumulation of reddish-yellow oil-globules, hanging together in clusters, in the vicinity of the vitelline disc; in gammarus pulex the vitelline globules included in the ovum along with the developed embryo, are large, and of a violet-blue, but the oil-globules are yellowish red; both refract powerfully. In many of the percidæ the oil of the yolk is amassed into a single large drop; and in the yolk of the emys Europea, according to Purkinje, the oil is collected into four or five distinct drops. On the chemical peculiarities of the oil of the vitellus, and indeed the whole chemical analysis of the ovum, vide Berzelius' *Animal Chemistry (Thierchemie*, 1831, p. 539). Hitherto, in undertaking a chemical analysis of the egg, there has been no attempt made to separate the oil-globules from the proper yolk globules.

to resemble that of the bile (cholestearine). Exposed to a certain degree of heat, the yolk acquires a greater degree of consistency, and under the microscope exhibits numerous rhombohedral and octohedral crystals. Incinerated, the yolk yields phosphatic salts, particularly phosphate of lime, and traces of free phosphoric acid [66]. The fluid of the germinal vesicle appears to consist of pure aqueous albumen [67].

CHAPTER II.

GENERAL MORPHOLOGY OF THE SEXUAL ORGANS.

§ 22. So far as the anatomical relations of the sexual organs can be clearly and securely followed in the organic kingdom of nature, so far do we find an obvious separation into two sexes [68]; as a general law, the male and female reproductive organs are divided between two individuals; it more rarely happens that they are united in a single individual, which then constitutes a proper normal hermaphrodite. The sexual organs are invariably parted in man and the vertebrata, and no case of true hermaphroditism appears yet to have occurred among them [69]. In the invertebrate

[66] The relative proportions of the several proximate principles of the yolk, according to Dr. Prout, are 0,17 albumen, 0,29 oil or liquid fat, 0,54 water. The ultimate principles, on the same authority, are sulphuric acid, phosphoric acid, (and traces of their bases, sulphur and phosphorus,) chlorine, potash, soda, lime, and magnesia, the latter generally in a state of union with carbonic acid, also a trace of iron. The analyses hitherto published refer, almost every one, only to the yolk of the new-laid hen's egg. Comparative analyses of the yolk of the ovum still contained in the ovary, and of the changes it undergoes, are unfortunately still entirely wanting.

[67] The fluids contained in the germinal vesicle coagulate, as has been already stated, in alcohol and acids, acetic acid among the number, which frequently fails to cause any coagulation in other albuminous fluids. When coagulated, the contents of the germinal vesicle form an irregular finely granular mass. A representation of the appearances may be found in my *Prodromus*, fig. xi. *b*, fig. xxviii.

[68] It were out of place to enter here into a disquisition, either upon what is called equivocal generation, or on the fissiparous and gemmiparous modes of procreation observed among the lowest classes of animals, our business being with sexual generation only. Gemmiparous generation, too, is very frequently distinctly referable to reproduction from ova.

[69] There does not exist a single undoubted case of hermaphroditism in man or in the other vertebrate animals, the presence of the germ-preparing organs of the male and female being of course regarded as necessary to constitute that state.

series, also, division of the sexes is the general rule, which occurs in insects, arachnidans, the majority of crustaceeans, and many molluscs. Normal hermaphroditism, or that state in which spermatic fluid and ova are produced in one and the same individual, occurs, as it would seem, in conchylia; in many annellides, in the echinodermata, polypi, infusoria, &c., the two forms of sexual apparatus are found united, and lying at no great distance from one another. There appears to be no general rule applicable to these classes: closely allied genera frequently present themselves as sexually distinct in one case, as hermaphrodites in another. Among vegetables also, in the majority of instances, organs of two different kinds, which from analogy with the animal kingdom have been divided into male and female, appear to be necessary to reproduction [70].

All the cases of hermaphroditism hitherto observed have their grounds in defective formations of the sexual organs, or in permanence of some earlier stage of development, when the male and female organs still bear a strong resemblance to each other. Vide the critical remarks on the doctrine of hermaphroditism in Müller's *History of the Formation of the Genital Organs (Bildungsgeschichte der Genitalien,* 4to, Dusseld. 1830). The case observed by Rudolphi and described by him in the *Transactions of the Berlin Academy* for 1825, in which a testis and seminal conduits were found on one side, and an ovary and Fallopian tube on the other, is now rendered suspicious, like all the others, by the later researches of Müller. Cuvier speaks of hermaphroditic formations which he had observed in fishes *(Histoire Naturelle des Poissons,* i. p. 534); but here, too, a microscopical analysis, which was not made, would alone have been competent to decide the fact. Among several classes of the invertebrate series, insecta for instance, and among these particularly lepidoptera, abnormal hermaphroditic formation would appear actually to occur. On the subject of abnormal hermaphroditism in the animal kingdom, see the elaborate account by Burdach in his *Physiology*, vol. i. [See also the excellent article HERMAPHRODITISM, by Dr. Simpson, in Todd's *Cyclopædia*, vol. ii. which contains the details of a great number of cases, derived from various sources. Such close approximations to true hermaphroditism in the human subject have sometimes been made, that it would probably be rash to maintain the impossibility of such an anomaly ever occurring. R.W.]

[70] The subject of the reproductive organs of vegetables has been left, in what follows, almost entirely untouched; the contradictory character of the statements of the more recent inquiries, and the symptoms of an impending great revolution in the whole doctrine of the sexes of vegetables, made it impossible to approach this topic with any chance of profit. According to Schleiden's otherwise extremely interesting inquiries, it would appear that the pollen-capsule, instead of being the male, is much rather to be viewed as the female organ, being the part which furnishes the germ that is evolved into the embryo; Meyen and others, again, regard the fovilla of the pollen, as Brown, Brongniart, and others had done already, as the true semen, possessed of spermatic animalcules; finally, Valentin, whilst he agrees in the main with Schleiden's observations, rejects *in toto* the doctrine of the sexes of vegetables, and their analogy in this particular

§ 23. *Structure of the Sexual Organs in Man and Animals.*

The sexual organs of animals are naturally divided into GERM-PREPARING ORGANS—the testes and ovaria—which are essential, always present, and the analysis of which has just engaged us; TRANSPORTING ORGANS—vas deferens and oviduct; and EMITTING ORGANS—penis and vagina, which at the same time serve as implements of sexual intercourse. In addition to this associated system of parts, there are added a variety of accessory organs, such as a reservoir of the matters elaborated in the germ-preparing apparatus, or, it may be, a secerning organ; in this category are placed the vesiculæ seminales, and the various and very numerous glands denominated prostate, Cowper's glands, follicles of the vagina, &c.; these are often entirely wanting; in other cases they are highly developed[71].

§ 24. In the animal kingdom the testicles and ovaria are mostly formed after the same essential type, and in their structure bear all the character of organs of secretion: in many of the invertebrata—the acephalous bivalve molluscs, the crustacea, many insects, &c. —the testes and ovaria are either simple or ramified cœca, or pouches; in the hermaphroditic snails they form a common cluster; in those in which the sexes are separated, the testes and

with the members of the animal kingdom. Vide Schleiden in Wiegmann's *Archiv*, f. 1837, B. I. S. 289, and Müller's *Archiv*, f. 1838, S. 137, Valentin's *Repertorium*, f. 1838, S. 62. See also the observations already made under annotation 8 to § 5. In addition to the particulars just mentioned, and those referred to, it is necessary to state that Unger has lately published two valuable papers, accompanied by beautiful drawings, upon the spermatic animalcules of plants, in *Nova Acta Academiæ Cæsar. Leopold. Nat. Curios.* vol. xviii. (1837, pp. 687 & 786). In the first essay this writer describes very completely the seminal animalcules of sphagnum. In the second he gives delineations of those of polytrichum (which agree very much with those of sphagnum), and of marchantia. He has also found very similar bodies in other mosses (funaria and bryusca), and, besides marchantia, in grimaldia hemispherica. To examine these bodies it is necessary to seize the precise time at which the contents of the anthers attain their highest development. For polytrichum commune, one of the commonest mosses, the month of May is, according to Unger, the proper time for instituting researches.

[71] The brief summary contained in the immediately following paragraphs will suffice in this general physiological consideration of the morphology, inasmuch as, with the exception of testes and ovaria, the other sexual organs are really of little importance, and the insight into the nature of the reproductive process is not facilitated by any more particular consideration of them.

ovaria exhibit preeisely the same structure, and are only to be distinguished by the nature of their eontents. In fishes both organs present themselves as great saes, or flattened and elongated masses; in the stroma of the testis we usually meet with long eonvoluted tubes, more rarely small round vesieles; in the ovaria, on the other hand, we have shut eapsules; the resemblanee deereases when we eome to the mammalia and man; greatly elongated and extremely slender eanals, pressed and wound together like a skein of thread, and paeked up within a eommon membranous envelope or eapsule, is the eharacteristie structure of the testis; round, shut, raeemiform elustered, but not eommunieating eells, is that whieh is proper to the ovary. Both testes and ovaries in all the higher animals lie under the kidneys; in many mammalia, too, the testes as well as the ovaries are eontained in the abdomen, or they return into its eavity during the season of heat, so that the position externally of these organs is lost as a permanent eharaeter. The eonvoluted eanals of the testis seerete the semen, the elose ovarian eells the ova[72].

§ 25. In the higher vertebrate animals, and in many of the invertebrate series also, the seminal eanals or vessels open into a wider membranous eanal—the vas deferens, whieh eonduets the spermatie fluid outwards; the oviduet, however, the analogue of the vas deferens in the male, is not in uninterrupted eonneetion with the ovary; still it is so very generally among the invertebrata, and there is even a tendeney to eontinuity in many mammalia;—in the greater number of the earnivora, for example, a membrane proeeeds from the edge of the opening of the Fallopian tube, whieh surrounds the ovary in the manner of a bag or capsule, more or less eompletely. In many animals, as in fishes, the tubuli seminiferi and oviduets are extremely short, and are in faet no more than narrower proeesses or prolongations of the saeeulated testis or ovary; in many speeies even these are wanting, and the semen and ova are shed direetly into the abdomen, whenee they are extruded through peeuliar elefts in its walls.

[72] For an account of the various forms of the male spermatic organs, see particularly Müller's able woik, *De Glandularum secernentium Structura*, fol. Lips. 1830 (in English by S. Solly, 8vo. Lond. 1839). For details of the analogy in structure between the ovaria and the testes in the animal series, I beg to refer to my *Elements of Comparative Anatomy*, chap. vii. p. 290 et seq. (in German). Tables i. and ii. in Burdach's *Physiology*, vol. i. give a good view, or rather scheme, of the principal forms of testicle and ovarium observed in the animal kingdom.

Proper external organs of generation occur but in individual classes and orders of animals ; in the Mammalia they are general ; so are they also in the scaly Amphibia and in Insects ; they are much less general in other classes, in Birds for example, the smooth-skinned Amphibia, Fishes, &c. ; in the Snails they are met with commonly enough [73].

§ 26. The general consideration of the morphology of the human organs of generation, shows us certain relations which serve to elucidate many physiological phenomena. What we learn admits of application, and furnishes us with analogies in reference to the same system through the whole of the series embraced by the animal kingdom. The TESTICLE is composed of TUBULI SEMINIFERI, canals of great tenuity, which are every where copiously surrounded by blood-vessels. The tubuli anastomose with one another in loops. When unravelled from the tangled skein which they form naturally, they constitute a canal of the delicacy and diameter of a sewing-thread of more than a thousand feet in length ; the amount of secreting surface is consequently very considerable. The tubuli unite into a variable number of excretory ducts, which pass into a thicker convoluted and looped tube, the EPIDIDYMIS, which in its turn terminates in a simple contorted canal, the VAS DEFERENS, which at its terminal extremity is provided with a diverticular appendage, the VESICULA SEMINALIS. This last appendage seems to serve partly as a reservoir for the spermatic fluid, partly as an organ of secretion ; it is not found in many mammalia. The PROSTATE and COWPER'S GLANDS are secernent organs, the clear viscid secretion of which consists of a transparent liquid intermixed with flocculi and granules, which are mostly either normal or altered epithelial cells. The PENIS is a highly vascular organ, copiously supplied with nerves, which, in virtue of a peculiar and not yet perfectly understood mechanism of its blood-vessels, receives upon occasion such an afflux of blood, that it enlarges and stiffens, or undergoes erection, by which it is fitted to penetrate into the female vagina. The mucous or internal coat of the seminal vessels is furnished with a flattened cylindrical epithelium, which is continued into the vas deferens ; the epithelial cells of the vesiculæ seminales, which are tessellated or united in

[73] See the description of the various forms pertaining to these organs, in my *Elements of Comparative Anatomy*, and Burdach's *Physiology*, vol. i. On the remarkable forms they present in fishes, see the older as well as the more recent writings particularly referred to by Rathke, in his contributions to Burdach, l. c.

the manner of a pavement, contain nuclei of considerable size, and, farther, a quantity of granular matter [74].

§ 27. The OVARIA of the human female have a very compact and solid stroma; each ovarium contains about fifteen fully-formed Graafian vesicles, in which the very small ovula (measuring from the 20th to the 30th of a line) are imbedded in the manner already described; the FALLOPIAN TUBES, as well as the uterus, contain muscular fibres, which have the histological (structural) character of those of the involuntary muscles; the VAGINA is narrow at its orifice in the virgin, and partially closed by the HYMEN, which, however, leaves an opening of about half an inch in width superiorly; the CLITORIS is small; the mucous follicles situated between the labia and in the vagina secrete a fluid of a peculiar greasy odour [75]. The MUCOUS MEMBRANE between the labia pudendi, and covering the hymen and vagina to the middle of the cervix uteri, is covered with a tessellate epithelium; from the point indicated this is replaced by a cylindrate epithelium, which

[74] For further details concerning the male organs of generation, see the elementary anatomical works of Hildebrandt, by Weber, and of Krause. The best description and representation of the testis we possess, are those by Lauth, *Mém. sur le Testicule Humain, in Mém. de la Société d'Hist. Nat. de Strasbourg*, tom. i. liv. ii. 1833. He estimates the entire length of the seminal canals at 1750 feet; Krause thought that the mean length might be fairly stated at 1015 feet; the diameter of the seminal vessels varies from the twelfth to the sixteenth of a line, a statement with which my admeasurements coincide. Vide Krause in Müller's *Archiv* für 1837, S. 24. The vesiculæ seminales are wholly wanting in many animals, in the dog for example. Others of the accessory organs of generation, however, are very much developed in certain mammalia, for instance in the hedgehog, and many other insect-feeders and gnawers. Vide my *Elements of Comparative Anatomy*, § 256. With regard to the arteriæ helicinæ, the extreme divisions of which, associated in bundles like skeins of thread, have been held the efficient causes of erection, see Müller in his *Archiv* für 1835, S. 202, the dissentient observations of Valentin, and Müller's reply in the same periodical for 1838, pages 128 and 224. It seems very difficult to arrive at any thing like certainty in regard to the structure or disposition of the blood-vessels of the corpora cavernosa; I have not myself been able to come to any satisfactory conclusions; at present I look on the arteriæ helicinæ as retia mirabilia. See further under § 37. On the epithelial indusium of the male urogenital mucous membrane, see Henle's excellent Memoir in Müller's *Archiv für* 1838, § 112.

[75] Perhaps this peculiar-smelling secretion may be poured out by that pair of glands, the representatives of the glands of Cowper in man, which have been lately described by Mr. Taylor. These glands are considerably larger than in man, situated at the root of the corpora cavernosa clitoridis, and open into the vagina by excretory ducts of an inch in length. Vide Taylor, in *Dublin Journal*, 1838, copied into Schmidt's *Jahrb. f. Medizin*, Bd. XX. S. 5.

is continued through the tubes to the edges of their fimbriated extremities, where it passes into the tessellate epithelium of the peritoneum; the epithelial cylinders have similar nuclei, and carry cilia the $\frac{1}{300}$th of a line in length. In the mammalia, where the structures are all essentially the same as in man, the cilia may be seen many hours after death in rapid motion. After every menstrual period, certainly after every conception, the ciliate epithelium is thrown off and reproduced; the epithelium of the vagina is always in a state of copious desquamation. The ciliate epithelium is wanting before puberty, and after the period of childbearing is past; in animals it only makes its appearance when they have attained the age at which they can engender[76].

§ 28. *Comparison of the male and female Organs of Generation in the earliest periods of development.*

In man, and indeed in animals generally, the sexual organs are those that make their appearance the latest of any; they are even later than the kidneys and suprarenal capsules. In embryos of a month old there is still no trace of organs of generation to be discovered, although at this period the brain, spinal cord, heart, lungs, intestinal canal, liver, &c. &c. are plainly enough evolved. A pair of organs, peculiar to the fœtus in the very earliest stages of its existence, the corpora Wolffiana (§ 61, fig. LXXXV. *f*), occupy a conspicuous place in the abdomen, being situated one on either side of the vertebral column. It is in the course of the sixth week, when the corpora Wolffiana have already begun to decline in size, that the germ-preparing organs first show themselves as a couple of minute points on the upper and inner edge of these bodies; to the outside and upon or within the excretory ducts of the Wolffian bodies, a couple of threads next make their appearance, which gradually increase in size, become hollow, and finally change into the vasa deferentia or Fallopian tubes; they open downwards along with the ureters into the cloaca or *sinus urogenitalis* of Mül-

[76] See the account of the epithelium of the genital system of the female in Henle, loc. cit. Henle states that even on the outer surface of the fimbriæ of the tubes, there are still ciliate epithelial cylinders to be detected. I have always supposed, at least in animals, that I could observe the sudden cessation of these at the peritoneal edge. To observe the play of the cilia, and study the structure of the epithelium, let a full-grown rabbit be taken, which is not pregnant, and has not too recently had young. On the subject of the ciliary motions, see the third Book of this work.

ler, which receives at the same time the termination of the intestine and the excretory duct of the Wolffian bodies, and in the first instance forms a blind sac; for the anus only appears at a later period. By degrees the intestine recedes, as it were, from the sinus urogenitalis, and thus the perinæum is formed; the anterior part of the sinus again is transformed into the bladder, and its middle part in the female into the uterus. Simultaneously with the development of the internal organs of generation, namely, during the sixth week, a small prominence makes its appearance immediately in front of the depression that indicates the anus; this is the penis or clitoris, which soon shifts its place, comes much forwards, and exhibits underneath a canalicular depression; by the end of the second month, two folds have sprouted up on either side of this organ, which by and by show themselves as the scrotum or labia majora, according to the sex. In the second month it is still impossible to distinguish between the sexes of embryos (figs. XCI. XCII. XCIII. and CI.); it is only in the middle of the third month that recognizable diversities in point of form announce diversity of sex; the period at which differences in point of structure proclaim the same thing is still considerably later; at the tenth week the two sexes still bear the strongest resemblance to one another (fig. XCIX. and C.). The testes become rounder, the ovaria longer; both, especially the ovaria, retreat backwards towards the sinus urogenitalis, which, when the sex is feminine, now begins to be transformed into the uterus, and to be drawn out into cornua, from which the round ligaments arise, and run towards the inguinal canal; the oviducts and seminal ducts (Fallopian tubes and vasa deferentia) become strikingly different, and the latter are connected with the testes by the medium of the epididymis. In the fourth month the canalicular cleft of the penis is closed and becomes the urethra; on the clitoris, on the contrary, the edges of the cleft rise more and more, and become the labia minora. At the beginning of the fifth month the penis and clitoris are still very much of a size; in the course of this month, the lateral folds coalesce in the middle line, by which the raphé and the scrotum are formed in the male, whilst in the female embryo the labia majora are produced from these lateral folds, and cover and conceal the clitoris more and more. The vesiculæ seminales first appear in the fifth month, and arise as offsets from the extremities of the vasa deferentia. The testes continue within the cavity of the abdomen till the end of the seventh month; they then descend

through the inguinal canals, and in the ninth month attain the bottom of the scrotum (the descent of the testicle)[77].

CHAPTER III.

PHŒNOMENOLOGY OF THE GENERATIVE ACT.

§ 29. *Encounter of the Generative Elements.*

In entering on the consideration of the phenomena which compose the generative act, it is well to meet at the outset the principal questions which must necessarily be answered before any closer insight into the nature of the process can be obtained. The most weighty question of all this is—Must the generative elements which are severally prepared in the male and female sexual organs come into actual contact to produce their peculiar effects? and, the answer being in the affirmative, how and in what way is this contact accomplished? The decision of the point involved in this question is linked with extraordinary difficulties in man and the higher animals; so that we must turn to the remoter circles of organic nature for facts and observations to guide us in security along this obscure province of physiology. In the vegetable kingdom the researches of very recent times in regard to the sexes of plants have demonstrated the occurrence of an intimate material

[77] A very important paper by Valentin on the development of the follicle in the ovary of mammalia, has lately appeared (Müller's *Archiv* f. 1838. Heft. V. S. 526). The earliest histological metamorphoses are there traced with greater care than had hitherto been done. The testes and ovaries are evolved after the type of glands in general: lappets appear in a blastema, which change into canals. The difference between the two organs occurs subsequently; in the testis the seminal tubes are formed, and they become united to the vas deferens; in the ovary blind tubuli arise stellated from a solid mass in the centre; in these tubuli the follicles are first formed, after which the tubuli disappear. The interior of the tubuli, as well as that of the seminal canals, is beset with epithelial globules. In spite of everything that has been done, however, the evolution of the germ-preparing organs has not yet been followed with all the attention that seems desirable. The observations of Valentin were principally made upon young embryos of the sheep.

The subjects treated of in this paragraph will be found again touched upon in our history of Development, particularly in § 74. Vide Müller's history of the development of the genital organs (*Bildungsgeschichte der Genitalien*, Düsseld. 1830), and the brief but very clear account of the subject in Lauth's *Manuel d'Anatomie*, t. ii. See also the figures under § 73 and § 74. XCIX.—CIV.

contact between the pollen granule with its fovilla, and the nucleus of the ovum; as soon as this, and only when this has been accomplished, is an embryo evolved [78]. Among the lower orders of vertebrate animals, as in the frog and toad, we see the male seated on the back of the female, and shedding the semen over the ova at the moment they leave, or immediately after they have left the cloaca; the union of the sexes here continues for a shorter or longer time, —for hours or weeks, but always as long as ova are extruded [79]. In osseous fishes, among which no kind of embrace takes place, careful observers have seen that the females are followed by the males, that they turn their bellies to each other, rub the anal orifices together, and that the semen of the milt-fish is shed during the time when the roe-fish is depositing her spawn [80]. Among invertebrate animals, snails and insects are frequently observed in intimate conjunction for hours together; the coitus ended, or the creatures separated, the spermatic fluid will be found in appreciable quantity collected in particular sacculi, or receptacles of the female, the outlets from which are so placed that the ova, as they are extruded

[78] In vegetables, the peculiar material incident by which the pollen capsules are conveyed, often by a very lengthened route through the cellular tissue of the style to the receptacle, and through the opening or micropyle of the embryonal sac to its nucleus, has been placed beyond the reach of question by the observations of Brown, Brongniart, Amici, Corda, Schleiden, Wydler, Valentin, and others. It is only in regard to the organ or element that is actually developed into the embryo, that unanimity of opinion has not yet been obtained. After the occurrence mentioned, however, and only then, is it that the embryo begins to be evolved.

[79] In regard to the frog, the excellent researches of Roesel, in his *Historia Ranarum nostratium,* fol. Nürnb. 1758, may satisfy whoever has no leisure or inclination to undertake inquiries for himself. In the green frog (Rana esculenta) the male must often continue his embraces of the female for thirty or forty days, the exclusion of the ova from the cloaca extending over this interval of time. In the brown frog (braunen grasfrosch), the ova of which are extruded in a single mass in the course of a quarter of an hour, the connection is much shorter; as soon as the ova are fairly expelled, the male discharges his fecundating fluid over them, and immediately afterwards quits the female. In the tree frog the pairing lasts about three days and nights before the spawn is shed; the period over which the shedding extends is very various, from two to twenty-four hours; if it proceeds too slowly, the male is apt to forsake the female before it is completed, in which case the last laid ova prove unfruitful. Precisely similar circumstances are observed in regard to the bufonidæ and several other animals.

[80] On the pairing of fishes see the observations of Grant and of Argillander, as they are reported by Von Baer, but augmented by several peculiar to himself, in his *Researches on the Development of Fishes,* (Untersuchungen über die Entwickelungsgeschichte der Fische) Lips. 1835.

in succession, must necessarily glide past them [81]. These examples, chosen from very different groups of the organic kingdom, might be readily added to; they all tend to prove that in the generative act, under whatever variety of circumstances this takes place, whether with or without coitus, the semen and the ova are brought into mutual contact.

§ 30. It is infinitely more difficult to speak definitively as to what passes in the interior of the female organs of generation in the higher vertebrate animals. The older accounts of semen having been found in the uterus in the dead bodies of women, are unsatisfactory, inasmuch as the only certain means of distinguishing semen, viz. microscopic analysis, was not then employed. On the other hand, however, the presence of spermatozoa in the interior of the female sexual organs, after the access of the male, may be demonstrated by direct experiment in the case of birds and mammalia. Some of the older observers had already detected living spermatozoa, even several days after coitus, in the vagina and uterus, as high as the commencement of the Fallopian tubes of the bitch and rabbit [82]. More recent inquirers have amply authenticated these discoveries [83]; and there can now be no question but

[81] Audouin has called the bag or bladder in the female insect which receives the semen, *poche copulatrice*. If butterflies, chaffers, &c. be taken *in coitu*, this pouch will always be found full of semen, containing an abundance of active spermatozoa; see my *Contributions to the History of Generation*, (Beiträge, &c.) p. 560. A very complete anatomical and physiological paper of Siebold, assigns the receptaculum seminis as a very general structure among insects. Müller's *Archiv*, 1837, S. 392. See also Newport's article Insecta, in the *Cyclopædia of Anatomy and Physiology*, vol. ii. p. 993.

[82] In Leeuwenhoeck's unrivalled works there are many very remarkable observations on this subject, observations which have not been duly appreciated in later times. He caused bitches to be served several times with the dog, the last coitus being made to take place one or two days after the first, and he always found spermatozoa in great numbers, not only through the whole body of the uterus, but in both of its cornua, to the commencement of the Fallopian tubes. Vide *Opera Omnia*, i. p. 149. Observations of the same kind were made on rabbits, *ibid.* p. 66.

[83] The researches of Prevost and Dumas, which have been confirmed by myself and others, are very conclusive. The physiologists named, on opening the bodies of bitches and female rabbits twenty-four hours after coitus, found spermatozoa in numbers, and moving with vivacity in the horns of the uterus; there were none in the vagina; on many occasions they perceived a thin transparent serous fluid in the capsule around the ovary, but no spermatozoa. In bitches, so long as three and four days after coitus, the Fallopian tubes were still found to contain spermatozoa in small numbers; the cornua of the uterus, however, contained many, which were extremely lively; but in the fluid from the precincts of the

that the facts as particularly stated in regard to the dog and rabbit, are quite general. Spermatozoa may be found in the recently dead bodies of almost all animals that are frequently in heat, and produce several litters in the course of the year. In the female rat and mouse, for instance, it is very common to find spermatozoa, so easily distinguished in these creatures by their highly characteristic forms, lying in masses within the cornua of the uterus, and even in contact with the ova which have but just entered them[84]. In birds, also, the same circumstances are frequently to be observed. In a general way, indeed, success has not attended the attempts that have been made to trace the spermatozoa to the immediate vicinity of the ovaria; still, in several instances, recent observers have actually discovered spermatozoa within the capsular prolongations of the Fallopian tubes that inclose the ovaria[85].

ovaria there were never any to be discovered. Even on the sixth and seventh day spermatozoa could be distinguished in the cornua, but their number was now much diminished; in the tubes none were to be found. *Annales des Sciences Nat.* tom. iii p. 119—122.

84 Vide my observations on the rat, in Froriep's *Neue Notizen*, Bd. iii. No. 51. July, 1837. Between ova which had but just become attached, I found masses of spermatozoa of the characteristic forms already described.

85 Dr. Bischoff, of Heidelberg, lately communicated the following observation to me by letter:—" I have now," says he, " completely satisfied myself that the spermatic fluid reaches the ovary. After having repeatedly found spermatozoa in the vagina, and particularly, though no longer alive, in the Fallopian tubes, in bitches, some time after the intercourse of the male, I was at length so fortunate as to discover the fact I have announced, in a bitch which had been in my possession previously to falling in season for the first time, and which I knew for certain to have been lined first on Thursday, the 21st of June, 1838, at seven o'clock in the evening, and again on Friday, at two o'clock in the afternoon. This bitch was examined half an hour after the last encounter; I found spermatozoa alive and active in the vagina, in the uterus, through the whole length of the tubes and between their fimbriæ, and finally in the sac or capsule which the peritoneum forms around the ovary, and even upon this organ itself. There could be no doubt of the fact as I state it. I have preserved the other cornu of the uterus in spirit; perhaps spermatozoa may yet be recognizable in it." I myself made an observation on the 3rd of December, 1838, which confirms this of Bischoff in almost every particular, which in fact differs from his in little, save as regards the time at which it was made, but may not perhaps be considered the less interesting on that account. The subject of my observation was a bitch which had been kept at the anatomical theatre of this place for the last four years, and which had already littered eight times (the last time in the spring of the year). This bitch had been observed to be in heat for eight days; she was served in my presence at one o'clock, p. m. and immediately after the coitus, which lasted some twelve minutes, was at an end, she was shut up. After the lapse of exactly forty-eight hours, the animal was destroyed and examined. The vagina was found somewhat bloody, but otherwise dry; indi-

§ 31. That immediate contact of the spermatic fluid with the ova is necessary to fertilize these is farther shown by the experiments on artificial impregnation which were performed by the inquirers of the last century with every precaution and great diligence. In regard to vegetables, it has been long since proved that artificial fertilization was readily accomplished in diclinial (monœcious and diœcious) plants by transferring the pollen of the

vidual spermatozoa were found lying everywhere between the large epithelial scales; these spermatozoa were all dead. In the uterus the number of spermatozoa was greater, and here they were all alive. The number and activity of the spermatozoa increased conspicuously in the cornua of the uterus and in the Fallopian tubes; but it was at the abdominal end of the tubes that the animalcules presented themselves in greatest abundance; here they completely filled every depression of the mucous membrane in aggregated masses; their motility continued for three hours in albumen on the stage of the microscope. In the capsule or pouch around the ovary I did not discover any spermatozoa, but I saw many full of activity and vigour among the fimbriæ, on the right side and close to the ovary, in which there were three Graafian vesicles very prominent, one of them having even already given way. On the left side there were no spermatozoa found betwixt the fimbriæ, but many at the abdominal opening of the tube. In the ovary of this side there were two Graafian vesicles ready to burst. The cilia on the mucous membrane of the fimbriæ were in lively action, but what seems remarkable is this,—that though I could readily trace the cylindrate epithelium through the whole uterus and tubes, yet it was uniformly without cilia. In the vagina there was nothing but tessellate epithelium. The slightly milky fluid (milky from the admixture of oily particles), which was believed by older observers to be semen, filled the capsules about the ovaries, especially the one on the right side, to the amount of several drops; it, however, contained no spermatozoa.

[Dr. Martin Barry has also observed spermatozoa on the ovary. His words are: "in seventeen out of nineteen instances in the rabbit, though the parts were generally examined while still warm, I was unable to discover spermatozoa in the fluid collected from the surface of the ovary. In the other two instances, however, spermatozoa, or at least animalcules exactly like those I had been accustomed to meet with in the uterus and vagina, were really found on the ovary. I should rather say, that on one of those occasions spermatozoa were seen, while on the other it was a single spermatozoon that was observed. Some of the former were alive and active, though not in locomotion; others were dead. In that case, twenty-four hours *post coitum*, there was neither enlargement of the Graafian vesicles, nor a high degree of vascularity in any of the parts. In the other instance the single spermatozoon found was dead, and the ova had escaped. * * * * Whether the seminal fluid penetrates into the interior of the ovary, I am unable to determine; but certainly the changes above described, as taking place *post coitum*, in the condition of the ovum, while still in the ovary, are too remarkable not to favour the supposition that it does." *Researches in Embryology*, second series, *Phil. Trans.* for 1839, p. 315. It is worth noting that the observation of Bischoff, recorded in the preceding part of this annotation, was made on the 22nd of June, 1838; those of Dr. Barry on the 5th and 6th of September, and that of Professor Wagner on the 3rd of December, in the same year. R. B. T.]

one flower to the stigma of the other. The ova of frogs, toads, newts, and different fishes, are in like manner readily fertilized by having a little of the spermatic fluid of their several males passed over them; and even among mammalia impregnation seems actually to have been effected by the injection of spermatic fluid by artificial means into the vagina [86].

§ 32. Experiments of an opposite character, or in which the male sperma is prevented from reaching the ova, prove that material contact is indispensable to fecundation: the ova of the frog and of fishes, unless brought into contact with the sperma of their several males, remain unfruitful [87]. Among birds, the general rule is that no eggs are laid unless fecundation by the male has taken place; still it often happens that the common fowl lays eggs without having been trodden by the cock; these eggs, however, are

[86] The experiments of Koelreuter on vegetables ("A short Account of certain Experiments in regard to the Sexes of Plants, Lips. 1761," and "three supplements, ib. 1763—66." in German), deserve to be mentioned; as also those of Conrad Sprengel ("The Secrets of Nature discovered in the Structure and Fertilization of Flowers, Berl. 1793," in German). The "Biologie" of Treviranus contains a complete summary of these matters, as also of the subjects handled in several of the succeeding paragraphs of the text. On the artificial fertilization of the ova of frogs and toads, see the classical work of Spallanzani—*Esperienze, &c.* There, too, Spallanzani relates the remarkable case, in which, by means of a syringe, warmed to 30° R. he injected the spermatic fluid of a dog which had had an emission, into the vagina and uterus of a bitch in season, the animal having been as many as thirteen days confined previously to coming into heat, and the experiment being performed on the twentieth day, when the œstrum was at its height. Two days after the injection the animal ceased to be in heat; after a lapse of twenty days the abdomen began to enlarge, and on the sixty-second day she produced a litter of three puppies, two males and one female, which were very lively, and in their general shape and colour very much resembled not only the mother, but the dog from whom the spermatic fluid had been obtained for the experiment. The bitch was of the poodle breed, and had already had a litter. Professor Rossi, of Pisa, is said to have repeated this experiment with success: *Opuscoli scelti di Milano*, t. v. p. 96: in the translation of Spallanzani into German, p. 343. Rusconi has fertilized the ova of the tench (cyprinus tinca) artificially: he compressed the abdomen of the female at the spawning season, and received the ova as they fell from the anus into a vessel of water; he pressed the abdomen of a male fish in the same manner, and caught a few drops of the seminal fluid in the same vessel; the fluid diffused itself as a slight cloud in the water, and actually impregnated the ova. Müller's *Archiv* für 1836. S. 278.

[87] Here, too, the experiments of Spallanzani are highly important. He inclosed the lower part of the body of a male frog in a pouch of oil-silk; the animal copulated with the female as usual, plenty of spawn was laid, but not a single ovum came to anything. On examining the oil-silk covering, he found the spermatic fluid clinging in drops to its interior.

unfecundated and not proper for incubation; they spoil rapidly instead of producing a chick when set under the parent[88].

§ 33. We know that among many of the lower Vertebrata the ova of the female are extruded before fecundation has taken place, and that therefore the separation of the ova from the place of their formation is not in direct connexion with their fecundation. The extrusion of the ova in these cases is to be viewed rather as a consequence of the excitement arising from sexual intercourse. Among mammalia and in man, on the contrary, the rule would seem to be that no ova are detached from the Graafian vesicles unless fecundation has taken place. For this reason, that opinion appears improbable according to which the product of the ovary, even in those cases in which fecundation is accomplished internally, is cast loose to meet the sperma[89]. The grounds for believing that

[88] Baer, in his "History of Development" (*Enwickelungsgeschichte, &c.*), vol. ii. p. 24, says:—"The greater number of birds also lay eggs only after they are impregnated. In very productive birds, however, ova often free themselves spontaneously from the ovary, and it is well known that hens, which are amongst the most prolific of all birds, lay eggs even when they have had no intercourse whatever with the cock; these hens, however, begin to lay later than those that have been duly visited by the male bird. The same circumstance happens not very uncommonly among others of our domestic poultry. And individual instances of its occurrence are reported among birds in general."

[89] [The determination of the periods at which, and the circumstances under which ova are or may be cast loose from the ovary among animals, and especially in the human female, is a point of great interest, and may upon occasion become one of much importance. It is familiarly known and admitted that among the lower animals Graafian vesicles very generally burst, and of course shed their contents, towards the end of the period of heat, whether they have had connexion with the male or not. So long ago as the year 1672 the celebrated Kerkring (*Phil. Trans.* 1672.) maintained that ova were occasionally, at least, discharged from the ovary of the human female during the menstrual period. Subsequently it was several times observed that the ovaries of females who had died during the menstrual period presented appearances which could only be referred to the bursting of one of the Graafian vesicles. A remarkable case of the kind is recorded by Sir E. Home (*Philos. Trans.* 1817). Dr. Power (*An Essay on the periodical discharge, &c.* 8vo. Lond. 1832) seems to have been the first who ventured an opinion to the effect that the phenomena of menstruation were connected with the escape of an ovum from the ovary, but as this was strengthened by no particular facts, it can be viewed only as an ingenious conjecture. It was Dr. R. Lee (Art. OVARIA, in *Cyclop. of Pract. Med.* Lond. 1834) who from positive data—from repeated examinations of the bodies of women who had died while menstruating, and a comparison of the results of experience in reference to disease, and absence, and loss of the ovaria, first maintained that "all the phenomena of menstruation depend upon or are connected with some peculiar change in the Graafian vesicles, in consequence of which an opening is formed in their

the fecundation of the ovum takes place in the ovary are as follows: 1st. The fact that the semen penetrates to the ovary. 2d. The circumstance that the ova of birds, and also of mammalia, advance to maturity partially and in succession, and are also detached from the ovaria in the same manner, and that the fecundated ova in different families of the mammalia first make their appearance in the uterus after the lapse of a certain interval of time, more or less considerable, from the last visit of the male, an interval which is often so considerable as to render it improbable that the semen continues accumulated in the uterus during its course[90]. 3d. The occurrence of cases of extra-uterine conception, which are by no means unfrequent either in the human subject or among animals, speak loudly for impregnation of the ova in the ovary; in these cases the embryo commences and continues its evolution in the

peritoneal and proper coats." "Menstruation," he goes on to say, "probably does not take place during infancy, because the ovaria are not then developed; it is absent during pregnancy and lactation, because at these periods they are in a quiescent state; and after the age of forty-six the catamenia cease, because the parenchymatous structure of the ovaria has partially disappeared and the Graafian vesicles have degenerated." M. Gendrin (*Traité Philos. de Méd. Prat.* t. ii. 8vo. Paris 1839) has adduced several new and interesting facts which amply confirm these conclusions of Dr. Lee, without noticing them however; and he infers that "the menstrual hemorrhage is but the periodical expression of a function which begins with puberty and ends with the critical age, and that this function consists in the production and development of the ovarian vesicles;—it brings a vesicle, and therefore an ovum, periodically to maturity on the surface of the ovary, to be thence either expelled or destroyed by the rupture and the inflammation of the vesicle" (l. c. p. 29). Vide further on the evidences and effects of this periodical process, in the annotations under § 68. R. W.] Burdach enters fully into the reasons for and against this view, *Physiologie*, vol. i. § 292). He concludes that in absolute internal impregnation, as well as in that which is external, the product of the ovarium and the spermatic fluid come into immediate contact.

[90] In rabbits, ova are usually found in the cornua of the uterus on the third day after effective coitus; in the dog, and, it would appear, in the human subject also, the ova do not enter the uterus before the eighth day. Roe-deer are very remarkable in regard to the time at which the ova enter the uterus. Among these animals the rutting season, and with it sexual intercourse, occur towards the end of August and beginning of September; at this time Pockels found the uterus turgescent, full of blood, and the mucous membrane spongy; but he saw no change in the ovaria; immediately after this the turgescence of the uterus declines, and it is only at the end of December that the effects of the sexual intercourse begin to show themselves; there is now a fresh turgescence of the uterus, a grasping of the ovary by the extremity of the Fallopian tube, and enlargement of a Graafian vesicle; at the beginning of January the embryo, of extremely minute size, is discovered for the first time in the horn of the uterus. See Dr. Pockels' very interesting paper in Müller's *Archiv* für 1836. S. 193.

ovary or in the cavity of the abdomen, as the case may be, and often attains maturity with a perfectly normal condition of all its members. 4th. Direct experiments, which, though they are inadequate to decide, yet powerfully support this view: if the oviducts, or Fallopian tubes, be tied or divided in animals immediately after sexual intercourse, and before, according to the data supplied by observation, the spermatic fluid could have penetrated to the ovary, no fecundation, no development of ova follows; whereas the ligature or division of the same parts, if not performed for two or three days after coitus, has no influence in preventing the evolution of the embryo[91].

§ 34. It is not absolutely necessary in man and the mammalia that the male organs of generation should penetrate completely into the corresponding organs of the female, in order that impregnation may follow the sexual act; this indeed is facilitated by such

[91] The experiments of Haighton on rabbits are highly important: the division of one oviduct (Fallopian tube) performed from one hour and a half to four hours after coitus, prevented the bursting of the vesicles on both sides; if the operation was performed forty-eight hours after coitus, fewer vesicles burst on the injured side, and no embryo was developed; on the uninjured side however perfect fecundation followed. The division effected sixty hours after coitus had no influence in impeding the development of the embryos on either side. When coitus took place after the division and closure of one of the tubes, Haighton found a vesicle of the corresponding ovary ruptured, but no embryo was produced; on the uninjured side, on the contrary, impregnation and development followed as usual. Vide *Phil. Trans.* for the year 1797. These inquiries are often quoted amiss, and spoken of as if they favoured the opinion that the stimulus of the sexual act was regularly followed by the rupture of a Graafian vesicle. Vide § 41. [See also Dr. Blundell's experiments confirmatory of these views in *Medico-Chirurg. Transactions,* vol. X. The experiments of Haighton have been variously interpreted according to the views of individuals and to the appearances in the ovary which were held significant of impregnation. Dr. Haighton himself regarded his experiments as leading to conclusions other than those in the text; he says expressly that they "overturned any argument which has been adduced to support the hypothesis that the effusion of semen on the ovaries is essential to impregnation," which he ascribes entirely to *sympathy;* "the semen stimulates the vagina, os uteri, cavity of the uterus, or all of them; by sympathy the ovarian vesicles enlarge, project, and burst," &c.: here he assumes the presence of corpora lutea in the ovaries as indubitable evidences of impregnation having occurred; he sets out in his inquiries, indeed, with the axiom that "no corpora lutea ever exist in virgin animals," and therefore concludes that wherever they occur there impregnation has preceded. But having constantly observed that though corpora lutea presented themselves in the ovary of that side the Fallopian tube of which had been divided, no embryo was ever found there, whilst on the opposite side where the Fallopian tube was entire both corpora lutea and embryos were discovered in like numbers, he asks, "if

a penetration, but it is enough that the male sperma be simply so thrown or introduced into the female organs, as that it may by possibility reach the os uteri; this may happen without destruction of the hymen, the injection taking place through its opening; the continued advance of the spermatic fluid after this,—its passage through the uterus and along the Fallopian tubes,—is secured partly by the ciliary motions which begin in the cervix uteri, partly by the contractions of the tubes, and partly by the motility of the spermatozoa;—which of these various means proves the most efficient in accomplishing the purpose in question, cannot at present be determined. There are decisive cases as regards man, in which fruitful intercourse has taken place without actual intromission [92]; men with malformations of the intromitting organ,—with hypospadias and epispadias of the worst kinds; men who have had the penis partially amputated, in whom but a very imperfect coitus could take place, have all proved their capacity to engender [93]. Those cases, on the contrary, are highly improbable, and generally not well or truly reported, in which impregnation is said to have taken place along with entire closure of the vagina, with a completely imperforate hymen, or in which the external surface of the abdomen, or the clothes only, were wetted by the seminal fluid in the course of an incomplete or forcibly attempted coitus [94].

§ 35. We have now to inquire into the more immediate conditions necessary to fecundation as regards the quantitative and

the application of semen to the vagina or uterus be sufficient to stimulate the ovaries to perform their first procreative functions without enabling them to achieve any thing more? and does it require the active energies of the seminal fluid operating by direct contact on the surface of the ovaries to produce the full measure of their effects?" The answer we should give to these queries would be in the spirit of the text: the ovaries in a fertile female animal do already and of themselves perform their first procreative functions, i. e. they prepare ova and perchance even cast these loose during the season of heat or menstruation; and farther, the active energies of the seminal fluid, operating by direct contact with the surface of the ovaries or the ova, are required to have this first procreative function made effective, to have it followed by the development of an embryo. R. W.]

[92] Cases of the kind occur in many of the later as well as earlier writers (vide Burdach, *Physiologie*, i. 528). Very recent cases are related by Heim, Ribke, Casper, and myself. Vide Casper's *Wochenschrift*, 1835, Nos. 1, 3, and 29; Henke's *Zeitschrift*, 25tes *Ergänzungsheft*, S. 1.

[93] Burdach quotes the cases in which malformations of parents are transmitted as affording security against any possible mistake.

[94] In these cases of coalescence of the vagina and the like, there was undoubtedly always an opening, however small. Against the idea that impregnation can follow simple wetting of the linen, &c. vide Henke in his *Zeitschrift* f. 1837, S. 1, and the whole of my previous and further remarks.

qualitative relations of the sperma to the ovum, and the reciprocal influence of these upon one another. The chief conditions are: 1. That the ovum possess a certain maturity of its elements, especially, as it would seem, of its vitellus or yolk; it is not, however, always necessary that the yolk be completely developed in order that fecundation be effected. Among birds, for instance, several ova very unequally advanced, and that go on ripening gradually, and attain maturity in succession, are often fecundated at once; a great number, however, still remain unimpregnated in these cases, and do not advance. Among amphibia and fishes ripe ova only, and these even excluded from the ovaria, can be fecundated artificially; in man and the mammalia the ovarian vesicles that burst are the largest, and therefore it may be presumed the ripest. 2. The sperma must be recent. The fecundating power of the male secretion is not always lost suddenly, or even very speedily; and the period at which it ceases is different in different animals:—among frogs and fishes the sperma will still fecundate that was taken from the bodies of animals killed hours before. The power is probably in relation with and dependent on the vitality of the spermatozoa; these, as we have seen, are found alive and active after several days in the natural passages, especially amidst the slime of the uterus and tubes; they die very much sooner out of the body. 3. The quantitative relation of the sperma seems to have but little influence on its fecundating power; a very small quantity suffices among the lower classes of animals to fertilize a large number of ova; and in man and the mammalia it would appear that a much larger quantity is produced than is absolutely required, a large proportion of it being either lost externally, or remaining in the vagina and uterus unused; only a very small quantity comes into immediate contact with the ovaries. 4. The sperma must contain spermatozoa. These exist in numbers in the smallest globule of the fluid scarcely visible to the naked eye; hence the experiments on artificial impregnation that have been reported, in which this is said to have been accomplished with semen freed from animalcules, must be erroneous; there is, in fact, no means of separating the spermatozoa from the semen. 5. There is no invariable mutual relation observable betwixt the quantity of semen and the number of fecundated ova[95].

[95] The experiments of Spallanzani have also thrown much light upon the several particulars now enumerated. The spermatic fluid of frogs, toads, and so forth, will continue to preserve its power for eight hours after the death of the animal; dilution with water, bile, saliva, urine, and vinegar in small quantity, does not destroy the fertilizing power; Rusconi fecundated the ova of frogs with sperma

§ 36. It is impossible to speak of the material relation of the semen to the ovum after or at the instant of feeundation. The ideas of some recent as well as older observers that the spermatozoa penetrated the ovum itself, and were there developed into the embryo or the nervous system of the embryo, are altogether inadmissible. No seminal animalcule has ever been discovered with the aid of the best instrument in the vitellus, stratum vitellinum, &c. of the ovum; nor is it conceivable how these creatures should have power to penetrate the vitellary membrane. Seminal animalcules are indeed found in abundance, and even after they are dead, in the neighbourhood of the yolk-ball, but none within its substance[96]. The possibility of the transudation of the liquor seminis to the stratum vitellinum is not to be gainsaid, though the fact is not demonstrable by the microscope or otherwise. The notion that the vitellus, in the ovum of the frog, to quote a single case, has its peculiar furrowed formation to the end that the spermatic fluid may reach and more easily exert its speeific influence on every part of the vitellary substance is unlikely; the furrowed appearance of the surface of the yolk would rather seem to be the effect of fecundation[97].

taken from the bodies of males which were exposed in the market, flayed and ready for dressing; Jaeobi fecundated ova with the sperm of a earp whieh had been dead four days. The temperature has an influenee here; the feeundating power eontinues longer when it is cool. Spallanzani found that the ova of frogs were impregnated when he used three grains of semen diffused in eighteen ounees of water for his experiments; when the same quantity of spermatie fluid was mixed with two pounds of water, the fecundating power was very eonsiderably diminished, and still more so with three and four pounds; but nevertheless, even when the disproportion was so great as twenty-two pounds of water to three grains of semen, several ova were feeundated. The fertilizing influenee was the same whether the ova were kept plunged in the spermatic fluid for some considerable time, or only for an instant. Vide Spallanzani for further and still more varied details; also Burdaeh in his *Physiologie*, and Ruseoni in Müller's *Archiv* f. 1835, S. 207. Ruseoni found that the ova in the female frog were suseeptible of feeundation three hours after the animal had been deeapitated.

96 The statements of the older observers, that the spermatozoa penetrated the ovum, eontended for entranee into it, shut themselves up there, and so on, are of eourse pure fables. Prevost and Dumas in our own times have maintained that the spermatozoa afforded the basis of the nervous system, brain, and spinal eord, and that the rest of the embryo grew to these out of the female generative elements. I have never seen spermatozoa in the vitellus, but many times, and very plainly, in its immediate vieinity; for instance, in the albuminons layer of the fecundated fish's egg. In the last case they had perished.

97 Ruseoni, in opposition to Baer, is eorreet in viewing the furrowing or wrinkling of the surface of the yolk as an effeet of advaneing development after impregnation; it is a eonsequenee, not a eause or means of feeundation. Vide Baer in Müller's *Archiv* 1834, S. 48, and Ruseoni, loc. eit. p. 207.

§ 37. *Phenomena accompanying the generative act.*

Besides the essential, the necessarily inherent phenomena of impregnation, there is a series of accompanying phenomena, reflections as it were, in other organic systems, which play a secondary part in the generative act. To this series pertain those occurrences which have their ground in a participation of the nervous system, and which in an especial manner accompany the sexual act. It is of importance to have a clear apprehension of these phenomena, as they exert an influence on the due encounter of the generative elements—the ejaculation of the spermatic fluid, and the casting loose of the ova. The nerves of common sensation appear to be almost uniformly in a state of high excitement during the sexual act; an intense feeling of enjoyment is experienced, which mounts continually, and reaches its height at the instant of ejaculation; it is often so powerful, that it is followed by a state of temporary unconsciousness, or the individual yields so entirely to the sensation, that he is no longer susceptible of other impressions. Ejaculation is always an involuntary act; and the muscular action that effects it belongs to the class of motions which have been characterized as reflected[98]; that is, the sensory nerves of the glans penis transmit a peculiar sensation to the brain and spinal cord, and these reflect the impression upon the corresponding muscular parts of the genital system: the scrotum is drawn up tight around the testicles, the vesiculæ seminales and prostate are compressed by the levatores ani, and the spasmodic rhythmical contractions of the perinæal muscles, particularly the bulbo-cavernosi, effect the vigorous ejaculation of the spermatic fluid. This, according to rule, only occurs during the complete erection of the penis, by which it is fitted to penetrate some way, more or less, into the vagina. Erection is accomplished by the swelling of the corpora cavernosa penis, which become distended with blood. Whether the so-called *arteriæ helicinæ* are concerned in the phenomena of erection, or these are produced by simple distention of the venous network of the penis, is not yet determined[99].

[98] On the immediate conditions of reflected motions generally, see the Book on the Nervous System. It may be well to state incidentally in this place, that the whole doctrine of the reflex functions rests entirely upon an hypothesis, which, however, affords the best explanation that can be offered of many phenomena. Ejaculation also follows in coitus without intromission of organs, through the simple stimulation of the nerves of sensation; among animals of the most dissimilar kinds we often observe reciprocal excitement of the genital organs, before the actual performance of the sexual act: birds, fishes, &c. touch or titillate the external genital orifices, &c. &c.

[99] Vide § 26.

§ 38. In the female the sense of enjoyment *sub coitu* appears to be principally excited by the friction of the labia interna and clitoris, which are alike in a state of turgesence or erection: this nervous excitement, as in the male, often reaches such a degree of intensity, that a kind of syncoptic state is induced. The impression made is also reflected on the nervous parts of the internal organs of generation, but the nature and extent of the effects produced on these cannot be appreciated by reason of their situation. In all probability, in consequence of the reflected impressions upon the motory fasciculi of the organic nerves, the os uteri dilates for the reception of the ejaculated spermatic fluid. An increased secretion of the peculiar-smelling mucus of the vagina also takes place [100].

§ 39. The union of the sexes is brought about by the peculiar instinctive feeling or appetite designated the sexual propensity. This appetite has physical grounds as the cause of its normal appearance: the evolution of the male and female generative elements acts as a stimulus upon the germ-preparing sexual system, the nerves of which convey their excitement to the sensorium, where the stimulation becomes consciousness, and imagination is aroused. Imagination, again, may in its turn excite the sexual appetite without physical grounds [101].

§ 40. The various phenomena that usually accompany the sexual act are by no means to be regarded as circumstances essential to its end; they are generally, but certainly not invariably, associated with a prolific union. We have seen that impregnation may be effected in a purely mechanical or artificial way, when of course all the phenomena in question are wanting: women have borne large families, who never felt any satisfaction in the embraces of their husbands; and numerous instances have occurred among men, in which fruitful intercourse has taken place not merely without all sensation of pleasure, but with positive pain; also

[100] Perhaps the rupture of the Graafian vesicle in man and mammalia, the separation of ova from the ovaria in other animals, in consequence of the sexual act, is an action or incident to be referred to this law in the physiology of the nervous system. Vide the observations on reflected motions in the foregoing paragraph.

[101] Examples of purely physical excitement of the sexual propensity may be observed in many morbid irritations of the genital organs and the parts connected with them,—for example, in inflammatory affections of these parts in gonorrhœa, calculus in the bladder, ascarides in the rectum, &c. The occasional instances of strong sexual desire that have been observed in eunuchs, and in children before the age of puberty, indicate the existence of the sexual appetite without normal physical causes. Vide on this point the *Physiology of the Nervous System*, and the *General Physiology*, Book iv.

without actual penetration of the sexual organs, and consequently without that intimate mental and physical communion which ought to accompany commixtion of bodies, and is usually held to be a state necessary to generation. Let but the one essential condition, to wit, the contact between the spermatic fluid and the ovum, be effected (§ 31), and all is fulfilled [102].

§ 41. *Immediate consequences of Sexual Intercourse and Impregnation.*

The most immediate consequence of the sexual act is the loosening of the ova; among some of the lower animals, as among frogs, toads, fishes, &c. this even happens during the act; in other instances it occurs later, as among insects, birds, mammals, and man. The stimulus of the intercourse is felt by the ovary; in the ripe ova, fecundated or fit for fecundation, the germinal vesicle disappears. How this happens, whether in consequence of sudden rupture, or through rapid colliquescence and liquefaction, shrinking together, decrease of contents, or otherwise, cannot be positively determined. It occurs, or may occur, however, before positive fecundation or contact of the semen has taken place [103]. This much is certain, that the germinal vesicle is always found to have disappeared so soon as the ovum is cast loose from the ovary; in rare instances the germinal vesicle is even wanting in every ripe ova still attached to the ovary [104]. The contents of the germinal vesicle, in which, with the increasing ripeness of the ovum, more and more consistent granulations are evolved, at the same time that the germinal macula is often disintegrated or dissolved, are apparently poured out in the space occupied by the germinal layer or germinal disc (§ 17), and from the anatomical position must be deposited in its central part [105]. In the mammalia

[102] Examples of violation of the person, with consequent impregnation, are not rare, but they are inapplicable as illustrations here, inasmuch as the sensations proper to the sexual act are involuntary, and may be aroused at the moment of intercourse; in spite of the utmost extent of moral repugnance and disgust. The absence of the phenomena that usually accompany sexual intercourse is scarcely observed save among women, and is probably owing to some imperfection of physical constitution; these individuals nevertheless, as stated, seem to conceive as readily, and have often as large families as others differently constituted.

[103] For example, in frogs, fishes, &c.—See the earlier paragraphs.

[104] This I have observed in various animals: Baer mentions it in reference to birds.

[105] An increase of this kind in the quantity of granulations, with disappearance of the original macula germinativa, is very distinctly seen in the scaly amphibia,

a certain excitement consequent on the sexual act, perhaps due to the presence of spermatozoa in the uterus, is communicated to the tubes, which with their abdominal extremity approach the ovarium, grasp this body closely by means of their fimbriæ, and receive the ovulum as it escapes from the bursting Graafian follicle [106]. When this has happened, and fecundation follows, development commences immediately, and without any further influence of the engendering individuals. Among other animals, birds for example, a like attraction occurs between the oviduct and the ripe impregnated yolks; but here other circumstances must be superadded, such as oviposition, natural or artificial warmth, and so on, if the evolution of the egg is to proceed. Other consequences of sexual intercourse, consensual phenomena in the nervous system, are not essential to, and have no influence upon fecundation [107].

§ 42. *Superfecundation and Superfœtation.*

It may be assumed as a positive and indisputable fact as regards man and the mammalia, that with fruitful coitus the generative act is closed, and its end accomplished. The rule is, that as soon as ova have been cast loose, the heat ceases in female animals: bitches will not then suffer the approach of the male. Here the instinct ap-

and even in birds and the mammalia, they make their appearance in the shape of pale clear globules. See many of the figures in my *Prodromus*, and that of the rabbit's ovum represented in fig. LXII. With regard to the changes immediately consequent on the disappearance of the germinal vesicle, we are compelled to seek refuge among pure hypotheses; observation has as yet come to no conclusions on this point. The later researches of Schwann appear calculated to lead inquiry into another, and perhaps a more fruitful path than it has yet taken. It is possible, namely, that the germinal vesicle is the parent cell for new cells of the germinal membrane or blastoderma. The new granulations into which I saw the germinal macula of amphibia and fishes separate, are perhaps young cells within the parent cell, [a fact that has been confirmed by Schwann and Dr. M. Barry. See the account of his *Researches*, in subsequent annotations. R. W.]

106 It has been maintained that Graafian vesicles might burst, and corpora lutea be formed in consequence of the simple stimulus of the sexual act; this is doubtful,—at all events it seldom occurs, and is abnormal when it does. Vide § 33 and § 38. It is extremely rare to find traces of such an occurrence in prostitutes who have never borne children. For an account of the formation of the corpora lutea, and the changes in the follicles, see under the head of Development, § 68.

107 To this category belong such incidents as lassitude, somnolence, &c. in both sexes after intercourse. Any definite sensations, such as shuddering, unusual enjoyment, &c. &c. as indications or immediate effects of impregnation having occurred in women, are altogether fallacious, and nowise constant.

pears as the pure and immediate expression and effect of the material condition. In the human female it would seem to be otherwise; in her the sexual disposition appears rather to increase during the first weeks after conception has taken place, probably through the influence of the local irritation upon the fancy. If one or a first fruitful connexion be followed shortly afterwards, and *before the formation of the decidua*, by a second, in some rare instances SUPERFECUNDATION may ensue [108]. Once the decidua is formed, and the ovum has reached the uterus, fruitful intercourse is no longer possible, and the cases of SUPERFŒTATION which have been admitted under these circumstances are physiological impossibilities, so that the recognition of such a circumstance ought to be banished from midwifery and legal medicine. The cases described as cases of superfœtation are all referable to twin conceptions, in which one of the fœtuses has perished at some anterior period of the pregnancy, and has been more or less perfectly preserved [109].

[108] The only cases of superfecundation that can be safely trusted, are those in which a woman has had connexion with two men of different races shortly after one another, and has brought twins to the world, a circumstance of which several instances are recorded. Vide Burdach, *Physiologie*, i. 541. Negresses have occasionally produced a mulatto and a negro at a birth: they had had connexion with a European and a negro shortly after one another. Animals with double uteri, such as hares, occasionally furnish examples of the occurrence of superfecundation, if so much may be concluded from the very unequal development of the embryos contained in the two cornua of the uterus. It has been presumed that the same thing must be possible in those females who are abnormally formed and have a double uterus; but in no case of such a conformation has any admissible instance of superfecundation occurred; and it is even highly probable that in such instances a decidua is formed in both halves of the uterus, inasmuch as this membrane, as we shall see by and by, is produced independently of the ovum, and exists even in cases of extra-uterine conception. See further on this point the annotations under § 77.

[109] Concluding from the present state of our knowledge of the physiology of generation, I hold superfœtation to be an impossibility; Siebold of Dantzig is of the same opinion; he relates the case of a young woman twenty-five years of age, who was for the second time delivered of a boy at the full period, and on the third day afterwards, and with the last afterpains, produced a mass of stuff, which on examination proved to be a blighted, flattened fœtus, which might have attained to about the fourth month; it had been compressed between the walls of the uterus and the membranes of the embryo which had attained maturity, and there remained without putrifying, a circumstance of which instances enough have occurred in cases of extra-uterine conception. Siebold is disposed to refer all recorded cases of superfœtation to precipitated or retarded deliveries, or to defective observation. *Journ. für Geburtsh.* Bd. xvii. S. 334.

SECTION THE SECOND.

OF DEVELOPMENT.

STATEMENT OF THE SUBJECT, AND PLAN OF TREATMENT.

§ 43. The study of embryonic evolution forms one of the most difficult portions of physiology. The history of the development of the human embryo, our peculiar subject, is almost wholly unknown to us in its first and earliest periods, and even as regards those that are later there are many gaps still to be filled up. The reason of this lies obviously in the want of opportunity to institute observations in sufficient number on recent human bodies, and in the uncertainty that pervades all researches upon abortive ova, which are for the most part in a morbid state, and are consequently only fitted after long experience and under the guidance of a competent knowledge of the normal condition, to supply data that may be relied on. On these accounts inquirers both of ancient and modern times have had recourse to animals, the development of which obviously resembles that of man, and which afford an easy means of making observations to any extent. The mammalia have the closest affinities with man, and, naturally enough, were thought calculated to afford the best results; but here, too, many difficulties immediately presented themselves,—to place the considerable expense of such inquiries out of the question: the ova of the mammalia are exceedingly small, their passage through the tubes is followed with difficulty, the epochs of the first stages of their developement are not duly known, and even appear to differ in different individuals, and then the several orders and genera of animals vary so much in many parts of their development, that new difficulties arise in the way on this account. In the class of birds many of the obstacles we encounter among the mammalia are wanting, or at least do not present themselves nearly to the

same amount as in quadrupeds. Among vertebrate animals, too, birds in their mode of development approach the mammalia most closely; the evolution of the bird and mammal in its type and essence is precisely the same. On this account all the older as well as later observers, whose discoveries form epochs in the history of development, have made the evolution of the embryo of the bird the first and most particular subject of their studies. As the common domestic fowl is the bird the eggs of which are most easily procured, and also the most readily hatched, so it is upon the development of the embryo of the fowl that we possess the most extensive and complete series of observations[110].

§ 44. In the following section we shall pursue the plan which seems best calculated for instruction. Whoever would work out a knowledge of the development of animals generally for himself, must begin with the study of the chick, were it only for the reason that we possess the best descriptive works upon this portion of the subject. We shall therefore start with a connected exposition of the history of the brooded egg; and then follow with an account of the evolution of the human embryo, referring constantly to what has already been observed in the chick, and illustrating the earlier stages, and particular obscure or difficult points, by comparative references to the development of the mammalia. From the history of the development of other animals, we shall only select so much as throws particular light upon individual relations of the human embryo, and supplies resting-places in our progress through the study of the laws of our evolution[111].

[110] The value of the study of the embryo of the bird to the history of development is well expressed by Valentin:—"Unquestionably the class of birds is the centre around which all observations on development arrange themselves, and this not so much on account of any grounds intrinsic to this class, as by reason of extrinsic circumstances which are completely under our control. In no other class of animals do we possess the same facilities of procuring embryos in the various stages of their progress. Nowhere can we multiply and repeat our inquiries to the same extent as here. It was on this account that Fabricius ab Aquapendente began his investigations with the brooded egg, and that Harvey and Malpighi followed in the same course; it was in the egg that Wolff made his important discoveries in regard to the formation of the intestinal canal, of the blood, of the extremities and of the kidneys; and it was by the study of the embryo of the common fowl that Doellinger and his school in our own day were enabled to give a permanent foundation to the history of development as a science. The bird must, therefore, and on these grounds, be made the starting-point for all future inquiries, the norma and basis to which insulated facts in the development of mammalia and man must be referred." *Handb. d. Entwickelungsgeschichte;* Vorrede, S. x.

[111] The most complete, connected, and systematic exposition we possess of the

CHAPTER I.

HISTORY OF THE INCUBATED EGG. DEVELOPMENT OF THE CHICK.

Appliances.—Historical matters.

§ 45. The best season for studying the development of the chick is the spring, when fertile and fresh-laid eggs are to be had everywhere; they may be brought forward by artificial warmth, or by being set under a hen. The latter is the more advisable means for those who are otherwise fully occupied, and cannot give the attention necessary to maintain an equable temperature in the hatching machine. Hatching machines are found of various construction; generally they are double drums or vessels of tinned iron, lined or

history of the development of organized beings—of vegetables, animals, and man—is to be found in the *Physiology* of C. F. Burdach, ii. 2nd ed. 1837, with additions and contributions from K. E. von Baer, H. Rathke, E. H. F. Meyer, K. Th. von Siebold, and G. Valentin. The Manual of the History of Development (*Handbuch der Entwickelungsgeschichte,* 8vo. 1835) of the last-named writer is also very complete, and contains an excellent bibliography of the whole subject. In addition, the various papers and memoirs of v. Baer, Rathke, and Carus—men who have each contributed more or less to our stock of knowledge in regard to the development of all classes of animals—ought to be consulted. On the development of individual organs, Meckel, Rathke, Müller, Huschke, and others have particularly distinguished themselves. The several works in which their observations are contained, will either be referred to in their places under the appropriate paragraphs, or will be indicated in our later Books. [The papers of Dr. Allen Thomson in the Edinburgh *New Philosophical Journal,* vols. for 1830 and 1831, may also be referred to]. The third fasciculus of the Plates illustrative of comparative anatomy (*Erläuterungstafeln zur vergleichenden Anatomie*) of Carus may be mentioned as a general atlas illustrative of development in every class of animals. The following chapters give nothing more than a summary exposition of the History of Development. It is not even the business of an elementary treatise of physiology to follow out this subject to its remotest details, and to particularize the origin and progress of every individual organ. This rather falls within the province of general anatomy, and all the later manuals of this science include it. See particularly the edition of Hildebrandt's Anatomy by Weber, the Manual of Lauth and others. Burdach has exhausted the subject,—he has given all that is known upon it in the place indicated. In our Physiology of nutrition, of sensation, and of motion, the origin and evolution of the several organs concerned in these functions will, according to circumstances, be found referred to more particularly.

loosely filled in the inside with down, wool, or paper-shavings, among which the eggs are disposed, the space between the outer and inner wall being filled with water, and the whole kept at the proper temperature by an oil or spirit-lamp. The proper temperature is from 100° to 104° F.; a degree or two more hastens the development; above 110° F. the embryo commonly perishes; at 95° F. it is developed more slowly. In Egypt the poultry-yard is generally supplied from eggs hatched in ovens constructed for the purpose, which have been imitated in France, but do not appear to have come commonly into use there[112].

§ 46. *History.*

Access to good descriptions and faithful representations is almost indispensable in studying the history of development; yet are we still without any complete collection of figures true to nature of each stadium of this process, and of the different organs in their successive stages of evolution; fragmentary, and, in part, admirable representations, however, we can boast, both of remoter and more recent times. Among the earlier observers, Fabricius ab Aquapendente and Malpighi must be particularly mentioned; in the last century Haller, and still more Wolff, obtained great credit for their researches. The first scientific and complete series of observations, in which many thousand eggs were used, was made by Döllinger, Pander, and D'Alton. The researches of Von Baër form a new epoch in the history of development, as his work is also the most complete we possess on the subject. Particular por-

[112] To take a general view of the history of the development of the chick it will suffice to employ a couple of fowls sitting at the same time, on from a dozen to fifteen eggs each, according to the size of the fowl and of the eggs. The date, hour, and day, when each egg is set must be written upon it, and as one or more are removed for examination, one or more properly inscribed are substituted for them. In this way eggs of the most different dates are soon at command. It is only necessary, in substituting fresh eggs for such as are taken away, to warm them slightly by holding them for a short time in the hand, otherwise the fowls are apt to become restless, and even to forsake the nest. Four or five eggs ought to be left to come out. Baumgärtner in his *Observations on the Nerves and the Blood* (*Beobachtungen, &c.* Freib. 1830) has described a very simple brooding apparatus. Coste and Delpech in their *Recherches sur la Formation des Embryons des Oiseaux*, Paris, 1834, have described and figured another and more complicated machine. On the influence of different temperatures see Von Baër in his *History of Development* (*Entwickelungeschichte*, I. 2).

tions of the history of development,—the evolution and growth of individual organs or systems, &c., have been worked out with success by more than one physiologist in very recent times [113].

§ 47. *Structure of the egg as just laid.*

The egg of the common fowl is surrounded externally with a hard calcareous *shell* (fig. XX. *a*), which consists almost wholly of

[113] The posthumous tract of Fabricius, *De formatione Ovi et Pulli*, makes part of his collected works, *Opera omnia*, fol. Lips. 1687, and better in the edition by Albinus, fol. Leid. 1737. The figures are pretty numerous, but rude, and no longer of any use. On the other hand the many representations of Malpighi in his tracts *De Ovo incubato* and *De Formatione Pulli in Ovo* (*Opera omnia*, fol. Lond. 1686) may still be referred to, particularly if they be viewed along with the admirable commentary of Döllinger in his academical programma entitled, *Marcelli Malpighii Iconum ad historiam Ovi incubati spectantium censuræ specimen*, 4to, Wirceburgi, 1818. Haller's researches bear principly on the formation of the heart: *Deux Mémoires sur la Formation du Cœur dans le Poulet*, Lausanne, 1758; the same work appeared, very much extended, in his *Opera Anatomica Minora*, 3 vols. 4to, Lausanne, 1766. The study of the works of Casper Frederick Wolff must be recommended to every one. They are as follows:—*Theoria Generationis*, ed. nov. 8vo, Halæ, 1774, which is accompanied by two plates containing several figures of the chick in different stages of its development; *De Formatione Intestinorum, &c.*, in *Nov. Commentar. Acad. Petropolitanæ*, tom. xii. (1767), continued in tom. xiii. (1768). The Essay on the formation of the Intestines

Fig. XX.

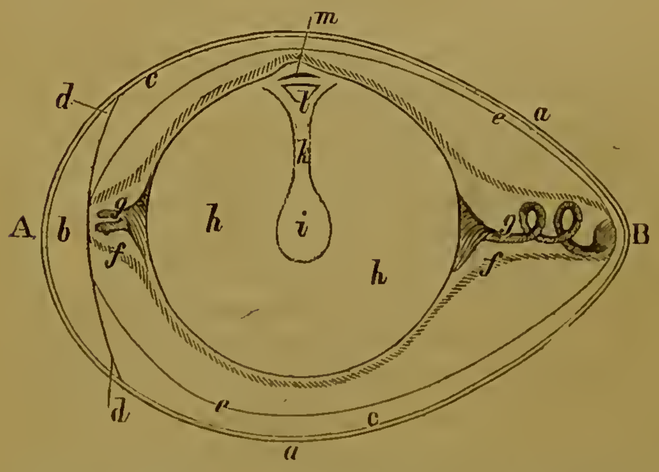

Fig. XX.—Ideal section of an extruded hen's egg, with slight alterations from Baër (*Entwickelung. der Thiere*, B. I. Tab. III) *A*, blunt pole; *B*, sharp pole; *a*, *a*, shell; *b*, space filled with air; *c*, membrane of the shell, which at *d*, *d*, splits into two layers; *e*, *e*, limits of the second and thicker albumen; *f*, *f*, limits of the third and thickest albumen clinging to the chalazæ; *g*, *g*, chalazæ; *h*, yolk; *i*, central cavity of the yolk, from which a canal or duct, *k*, leads to the cicatricula; *l*, cumulus proligerus; *m*, germ (blastos).

carbonate of lime. It is indeed without obvious pores, but is nevertheless permeable to air: some part of its watery constituent escapes during the process of hatching, and eggs that are covered with a coat of varnish die. Internally the shell is full of pits or depressions, in which small warty or shaggy processes of the lining *membrane of the shell* (the *membrana testæ*) are implanted (fig. XX. *c, c*). This membrane consists of two laminæ, the outer of which is made rough and uneven by the processes just mentioned; the inner, which is turned towards the white, is smooth and polished. The two laminæ separate at the blunt end of the egg (fig. XX. *d, d*), so that here they are most easily demonstrated, and contain the air-space, or *air-chamber (folliculus aëris)* between them, which first appears shortly after the egg is laid, and is very much enlarged by keeping and the heat of incubation. The membrane of the shell is formed of a compact fibrous tissue, and shows the chemical properties of coagulated albumen. Betwixt the membrane of the shell and the yolk is interposed the *white* (*albumen ovi*), the outer stratum of which (fig. XX. between *c* and *e*) is extremely watery and fluent, and consequently readily drained off when the shell is pierced; the inner layer, again, or that which lies nearer the yolk, is more viscid and thicker (fig. XX. between *e* and *f*), clings more closely to the yolk, especially by its inmost stratum, which immediately surrounds that part and the chalazæ

exists translated into German by J. F. Meckel, *Ueber die Bildung des Darmkanals, &c.*, Halle, 1812, with two plates. The best and most complete collection of figures we yet possess is that contained in the work of Dr. Pander, *Contributions towards the History of the Development of the Chick in the Egg (Beiträge zur Entwickelungsgeschichte des Hühnchens im Eie*, fol. Würzburg, 1817). The plates are by D'Alton, senior, and masterly in point of drawing. The work more particularly embraces the evolution during the first five days. The figures in the *Dissert. sistens Ovi Avium historiæ et Incubationis prodromum*, 8vo. Jenæ, 1808, by the Count von Tredern, are particularly neat in their execution, and extremely correct. Completeness of description was the object aimed at by Von Baër in his classical work entitled *Observations and Reflections on the Development of Animals, (Zur Entwickelungsgeschichte der Thiere, Beobachtung und Reflexion*, vol. i. 1828, vol. ii. 1837), and this he has fully attained. The extreme minuteness of this work, however, makes its study somewhat difficult, so that perhaps the compendious view or abridgment to be found in the second volume of Burdach's *Physiology*, is more to be recommended to beginners. The schemes or ideal sections of the chick given in both works are extremely useful in facilitating the comprehension of the subject. The figures of Coste and Delpech (op. cit. annot. 112) are in part incorrect, in part good. The figures incorporated in this work from fig. VIII. to fig. CXXVIII. supply whatever is most important to the illustration of the following descriptions, and are constantly referred to within brackets. I have followed Baër wherever it was possible to do so.

(XX. *f*, *f*). The white of an egg shows alkaline reaction, and contains albumen, salivary matter, and the common sulphates and hydrochlorates in small quantity. The *chalazæ* (XX. *g*, *g*, XXIII. *b*, *b*) are a couple of spirally-twisted ropes, composed of delicate fibres, or of a fine membrane, which, as the chalaziferous membrane (*membrana chalazifera*) closely surrounds the yolk, and then going off in the fashion of a funnel towards either pole of the egg, becomes twisted into a rope. (figs. XX. XXI. and XXIII.) A white streak, in the shape of a band, may usually be seen extending over the yolk from one chalaza to the other; this is the zone, or belt (*zona*), which, however, is not constant, and is of no particular importance. The chalazæ vary exceedingly in point of form and development; they appear to consist of coagulated albumen. The *yolk*, or *yolk-ball* (*vitellus*,) is somewhat lighter than the white, so that, in whatever position the egg is held, it always rises towards the side that is uppermost. The *vitellary membrane* (*cuticula vitelli*), (fig. XXII. *a*, fig. IX. *c*,) is a perfectly simple, transparent, and slightly glistening membrane. It surrounds the yolk (which with its central cavity, figs. IX. and XX. *i*, has been already particularly described, § 17) closely and immediately. Immediately under the vitellary membrane, and at a point which in an opened egg is always directed upwards,

Fig. XXI.

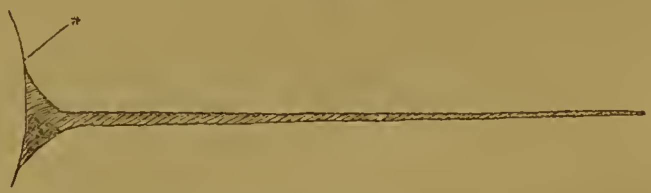

Fig. XXI.—One of the chalazæ of the Jackdaw's egg pulled straight. The way in which the twisted fibres of the part diverge into a funnel-shaped expansion as they approach the yolk, and so form the innermost stratum of the albumen, is displayed.

Fig. XXII.

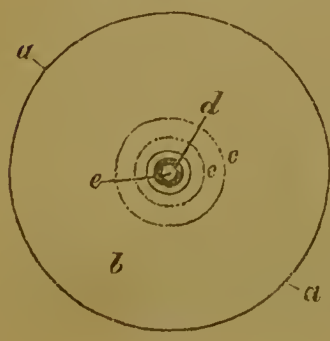

Fig. XXII.—Vitellus, or yolk of a hen's egg, seen from above: *a*, *a*, vitelline membrane; *b*, vitellus; *c*, *c*, halones; *d*, darker, more external part of the germ (the future area vasculosa); *e*, central transparent part of the germ (the future area pellucida). In the yolk here figured, the first slight effects of incubation are apparent, viz. in the separation in the germ, which often takes place from transient exposure of the egg to a high temperature (handling), or when the eggs have been laid some time and the temperature of the air has been high.

the *cicatricula* (fig. XXIII. *A, c,* and B), or tread, is seen shining through in the shape of a round whitish spot. The cicatricula consists superficially of a membranous stratum (stratum proligerum,—fig. XXIII. *B*), from a line and a half to two lines in diameter, in which the germinal vesicle was imbedded at an earlier period (§ 18). This is the *germ,*—blaste, s. blastos, from which in the beginning of the brooding the *germinal membrane,* blastoderma, is produced (fig. X. *A, b,* p. 40). The germ in recent eggs is generally slightly adherent to the vitellary membrane; in such as have been kept for some time, it is more detached; under all circumstances it is readily diffluent, little consistent. In the centre it is somewhat clearer and more transparent than elsewhere (fig. XXII. *e*), and allows the *germinal cumulus,—cumulus proligerus,* s. *nucleus cicatriculæ,* s. *nucleus blastodermatis,* also the *stratum proligerum* of Baer,—to be seen through it (fig. X. *A, d,* p. 40). This germinal cumulus is a loose whitish-yellow, and somewhat conically formed granular layer (fig. X. *A, d,* p. 40), sunk in the substance of the yolk; betwixt it and the discus proligerus, or germinal disc, there is a minute interval which is filled with a fluid that appears to communicate with the canal of the central cavity of the yolk[114].

[114] In the foregoing description and terminology, I have felt it my duty to follow Baer as closely as possible. Vide his 2nd vol. p. 10, et seq. On the chemical composition of the egg, see Berzelius, *Animal Chemistry* (*Thierchemie,* 1831), p. 537. The white consists of from 12 to 13 parts albumen, 85 water, 3 soda, common salt, and an extractiform matter; according to Bostock, it also contains salivary matter in considerable quantity, sulphates, and muriates; the

Fig. XXIII.

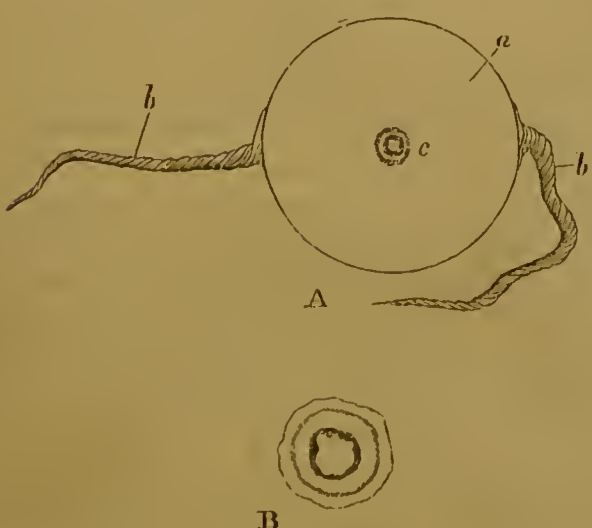

Fig. XXIII.—A, the unincubated yolk of the Jackdaw's egg *(corvus corone)*; *a,* the vitellus; the chalazæ, *b, b*; the cicatricula, *c.*
B, the cicatricula magnified.

§ 48. *Detachment of the ovum from the ovary, and completion of its formation in the oviduct.*

We have already spoken (§ 16) of the chorion, or outer-covering of the ovum in the ovary, coalescing with a layer of the ovarian stroma into a firm capsule or theca (fig. IX. *a*, p. 38). This capsule is surrounded externally with cellular tissue and blood-vessels, and is particularly thick in that part of its circumference towards the pedicle (fig. IX. *b*). The yolk, or vitelline-ball, lies within this capsule, and as it advances to maturity forms a more and more completely pediculated growth, like a berry, of which every ovarium presents many in different stages. (fig. XXIV.) On that side of each capsule, or berry, which is opposite the pedicle, a curved, pretty broad, white streak is observed; this is the *cicatrice*, (*stigma*), (fig. XXIV. *b*), which appears not to be vascular, for although the blood-vessels that enter by the pedicle form a conspicuous rete with rhomboidal meshes on every other part of the

alkaline reaction, Dr. Bostock also informs us, depends on the presence of free soda. The space which is filled with air, Bischoff says, contains a somewhat larger proportion of oxygen than the atmosphere.

[Dr. Paris published an analysis of this air in the year 1809.—*Trans. Linnæan Society*, vol. x. Before incubation it was atmospheric air; towards the end of the incubation it was the same air, but contaminated with a small portion of carbonic acid gas. R. W.]

Fig. XXIV.

Fig. XXIV.—Ovary of the Fowl, with vitelli or yolks, ripe and approaching maturity:—*a*, a ripe yolk within its calyx or cup, the cicatrice of which, *b*, *b*, is seen as a transverse vesselless streak; *c*, *c*, smaller yolks with the vascular rete of their cups and their cicatrices; *d*, a calyx empty, the part having given way along the line of the cicatrice; smaller yolks (*c*,) are enveloped by calices so transparent that the cicatricula is seen through them.

capsule, none is seen to cross or to penetrate the cicatrice. The capsule is thinnest at this point, and the yolk is here in most intimate contact, or even appears to be connected with it (fig. IX. at the lower part); the capsule at length gives way, yielding in the line of the cicatrice, and forming a transverse rent with double flaps, through which the yolk escapes. The rupture of the capsule in the line of the cicatrice is easily effected by slight pressure, even in ova that are far from maturity (fig. XXIV. *d*); it happens naturally to the ripe ova after impregnation. When the yolk has escaped, the capsule which had inclosed it presents itself as a hollow membranous funnel, the *calyx* (fig. XXIV. *d*), which remains hanging by its pedicle, and shrivelling up or shrinking into the stroma of the ovary, soon leaves no trace of its former existence. The detachment of the vitellus is accomplished either by the perfected growth of this body, its size proving sufficient at length to burst the cicatrice, or by an increase in the thickness of the capsule towards the pedicle, by which the vitellus is forced as it were against the cicatrice (fig. IX.); the whole process is very similar to that which occurs among the mammalia when the Graafian vesicle gives way and the corpus luteum is formed (vide § 67). The oviduct attaches itself, by a kind of suction, by its patulous infundibulum or bevelled abdominal end to the capsule which contains the ripest ovum, and receives this as it escapes. From this point the ovum makes its way moving spirally along the muscular oviduct, which is now very much enlarged, highly vascular, and pouring out from its mucous surface the albumen which is disposed around the yolk in the different layers but just described. The formation of the chalazæ is a consequence of the rotatory motion upon its axis which the ovum receives in the oviduct, and of the setting of the albumen. The lower part of the oviduct is dilated into a receptacle for the egg, and here are added the membrane of the shell, and finally the shell itself, the milky calcareous fluid secreted by this part being precipitated upon the egg in crystals, which are at first isolated, but very soon run together and cohere. The egg remains over twenty-four hours in the receptacle. The germ at the first entrance of the egg into the oviduct has already assumed the appearance proper to it at any period anterior to the commencement of incubation, the germinal vesicle having burst; the upper disciform layers of the germ and germinal cumulus only separate more and more. After the egg is thus perfected, it is forced rapidly through the cloaca. In other birds, it is here perhaps that the egg receives in part at least the beautiful

colours, red, green, yellow, brown, &c., in various shades, which are so frequently met with, and which appear to be so many tints of the colouring matter of the blood chemically altered [115].

Earliest period in the development of the Chick, from the first appearance of the Embryo to the first traces of circulation.

§ 49. The first period in the development comprehends about two days. In the first hours of incubation, the germ separates itself more from the vitellus and vitellary membrane, to which, however, it still continues in some sort attached; the germ acquires more of a membranous consistence, and the space between it and the germinal cumulus, which is filled with fluid, becomes somewhat larger (fig. X. *A*, p. 40). Towards the sixth, or between that and the eighth hour, a parting or resolution in the now foliaceous germinal membrane, which proceeds from the centre towards the periphery, is apparent ; a clear rounded space, about a line in diameter, is produced in the middle, this is the *area pellucida* s. *germinativa*,—the pellucid or germinal area (fig. XXII. *e*) ; the germinal membrane at the same time becomes darker in the circumference, and surrounds the transparent pellucid area like a ring, which is also about a line in breadth (fig. XXII. *d*) ; this is the future *area vasculosa*, or vascular area. The *cumulus proligerus* is seen in the deeper parts shining through the centre of the germinal membrane. At this time two or three annular lines appear drawn around the circumference of the germinal membrane,—the *halones* (fig. XXII. *c*, *c*) ; these are circular ridges or walls formed in the vitellus, between which there are furrows filled with thinner fluid. Now also the germinal membrane may be observed to show a disposition to separate into two layers, which are indeed still intimately connected, but even at this early period are in point of structure different. They are always particularized as the *laminæ* of the germinal membrane, the superior lamina being entitled the *serous* or animal *layer*, the inferior the *mucous* or vegetative *layer* ; the former is limited to the extent of the area pellucida, the latter extends farther in the periphery, stretching beyond the area vasculosa. The albumen disappears in a great measure over the germi-

[115] Vide the more particular details in v. Baer, and in my *Elements of Comparative Anatomy ;* also the beautiful figures in Carus's *Plates illustrative of Comparative Anatomy*, pt. 3. (Erläuterungstafeln) pl. viii. and the text, containing physiological observations on the origin of the colours of the eggs of different birds.

nal membrane, and the vitellus approaches the lining tunic of the shell more closely; in this situation, the vitellus becomes more prominent, forming a segment of a lesser sphere, like the cornea of the eye; a circumstance which may likewise be frequently observed in the egg before incubation (fig. XX. over *m*). It is not unimportant to observe that these, the earliest observable changes not unfrequently take place in eggs that are laid in summer and when the weather is very warm, though of course much short of brood-heat.

§ 50. About the middle of the first day, after from twelve to fifteen hours of incubation, the *blastoderma*, or germinal membrane, is completely detached from the vitellary membrane, and may be cut out as a connected lamina, and washed away from the membrane of the yolk (fig. XXV. and XXVI.). The *germinal area* (*area pellucida* s. *germinativa*) has now an elongated, often a somewhat pyriform appearance (figs. XXV. and XXVII. *b*), and is two lines in length. The darker *vascular area* (figs. XXV. and XXVII. *c*) has

Fig. XXV.

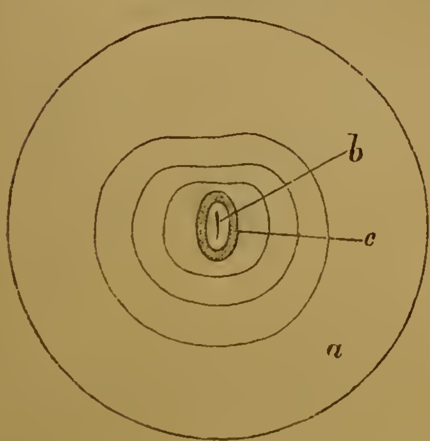

Fig. XXV.—Vitellus or yolk after from twelve to fourteen hours incubation, of the natural size (this and the other figures of the vitellus look larger than proper, from their having been placed in flat saucers to be drawn, by which they become somewhat flattened): *a*, the yolk; *b*, area pellucida, in the middle of which the *nota primativa*, or primary streak, the first trace of the embryo, is perceived; *c*, outer area pellucida, the future area vasculosa. The halones are indicated by the three concentric circles.

Fig. XXVI.

Fig. XXVI.—The same vitellus, but with a piece of the vitellary membrane and the subjacent blastoderma removed at *a*, by which the nucleus of the cicatriculæ, or cumulus proligerus, a dark disciform substance implanted in the vitellus, is brought into view.

also lengthened out, and the germinal membrane extends as a foliaecous formation indefinitely over it into the halones, which now begin to look less regular than they were originally. This outer portion of the blastoderma is called the *area vitellina.* About this period also the separation of the blastoderma, in the direction of its thickness, becomes more apparent; between the serous layer, which still continues limited to the germinal area, and the mucous layer, which extends into the vitelline area, there appears a new lamina, which, however, is only distinctly defined towards the periphery, where it approaches the limits of the area vasculosa; in the direction of the thickness this lamina lies in the blastoderma as if it belonged to both of the other layers, and penetrated into their substance; to distinguish this less separated lamina, it is spoken of as the *vascular lamina,* the blood and blood-vessels first making their appearance within its substance. This formation first becomes distinctly visible between the sixteenth and twentieth hour of incubation (fig. XXXI. *A, B, d*). Somewhat earlier than this, namely, about the fourteenth hour, the first rudiments of the embryo become distinctly visible in the middle of the germinal area, in the guise of a delicate white elongated streak, about a line and a half in length; it is designated *nota primitiva*—the primitive streak, and lies in the line of the long axis of the germinal area, which itself lies in the transverse axis of the egg (fig. XXVII. *a*). Under the nota primitiva, the cumulus proligerus, deeply seated, may still be seen very plainly glistening

Fig. XXVII.

Fig. XXVII.—Magnified view of the portion of the blastoderma removed in fig. XXII.—*a*, the nota, or primary streak; *b*, the oblong area pellucida; *c*, the oval area vasculosa.

through (fig. XXVIII. *A*, *B*, *d*). The nota primitiva rises slightly above the level of the germinal area (fig. XXVIII. *b*); it is thicker and blunter anteriorly, or towards that end which becomes the head of the embryo, thinner and tending to a point posteriorly. The nota primitiva is probably the groundwork of the brain and spinal cord[116].

§ 51. The nota primitiva, an aggregate of dark granules in the first instance, becomes more fluent by and by, and presents itself as a layer of delicate, transparent masses, by the side of which, between the sixteenth and eighteenth hour, a pair of new formations arise symmetrically, near the middle line. These are the *laminæ* s.

[116] In my view of the relations of the nota primitiva I differ from Baer, who regards it as the forerunner of the vertebral column, which speedily disappears again, whilst to me it seems only to undergo histological metamorphosis—*i.e.* to suffer change of structure in the course of its development.

[According to Reichert (*Entwickelungsleben im Wirbelthierreich*, 4to. Berl. 1840), the nota primitiva in the ovum of the frog is not raised, it is on the contrary depressed—a furrow or channel (S. 105); neither is it the rudiment of any part, but a mere indication and effect of a certain amount of formative process achieved, this process having reference to the primary halves of the central nervous system. R. W.]

FIG. XXVIII.

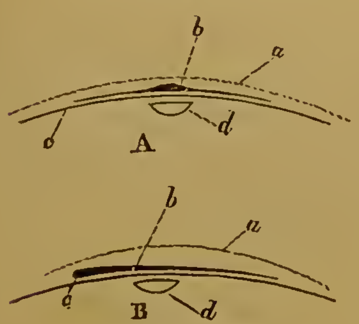

Fig. XXVIII.—Ideal sections of fig. XXV. (after Baer, with slight variations).—*A*, transverse section; *B*, longitudinal section; *a*, vitelline membrane, indicated by a finely dotted line; *b*, nota, or primitive streak, with the serous layer of the blastoderma, corresponding to the area pellucida; *c*, mucous layer of the blastoderma, corresponding to the area vasculosa; *d*, cumulus proligerus s. nucleus cicatriculæ.

FIG. XXIX.

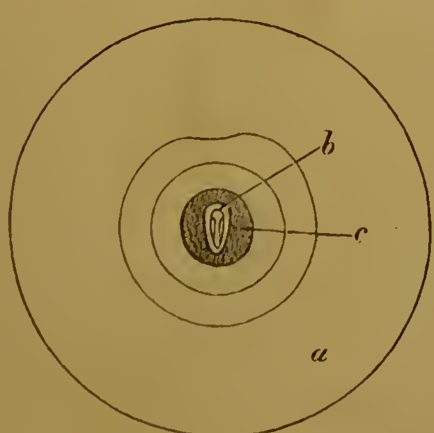

Fig. XXIX.—Yolk of the natural size, after eighteen hours of incubation: *a*, vitellus; *b*, area pellucida; *c*, area vasculosa.

plicæ dorsales—the dorsal laminæ, two cylindrical rolls or enlargements, which arise parallel to the nota primitiva, and form a couple of eristæ, or ridges, one on either side of it (fig. XXIX. and XXX. *b*, *b*), which diverge anteriorly and posteriorly, being nearest about the middle of their length, and sloping somewhat from without inwards, or towards one another. The angles of the ridges are softly rounded off; each ridge has the appearance of a clear broad line, which is ineluded within two darker lines. The germinal area presents a pyriform outline (fig. XXIX. and XXX). Under the canal for the spinal cord, which is bounded by the dorsal laminæ, we observe the *chorda dorsalis*—the dorsal cord (fig. XXXI. and XXXIV. *A*, *e*, and fig. XXXIII. *f*), an extremely fine elongated streak, surrounded by a transparent sheath; both the dorsal cord and the sheath go to constitute the cartilaginous column which appears later, and out of which by its becoming divided into pieees, the vertebral column is produced. The embryo with its laminæ dorsales now bends itself forward, at the same time that it here forms a sickle-shaped transparent fold (fig. XXX. *c*), the future *involucrum capitis*—the cranial envelope or cap. From the

Fig. XXX.

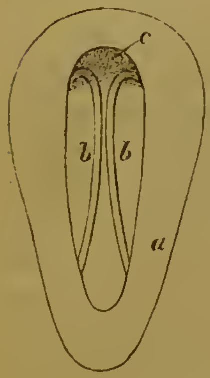

Fig. XXX.—The pellucid area of fig. XXIX. magnified: *a*, the pellucid area, now become pear-shaped; instead of the nota, or primary streak, the two dorsal laminæ or folds (*laminæ* s. *plicæ dorsales*) *b*, *b*, are seen; the involucrum capitis, or cranial envelope, *c*, a falciform fold, or kind of reflex blastoderma, begins to be developed.

Fig. XXXI.

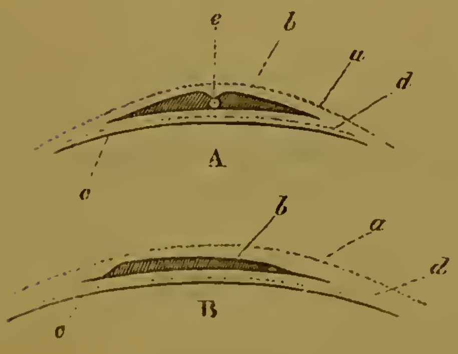

Fig. XXXI.—Ideal sections of figs. XXIX. and XXX.—*A*, tranverse section; *B*, longitudinal section; *a*, vitellary membrane; *b*, serous layer of the blastoderma, or germinal membrane, depressed in the middle by reason of the rounded elevations of the dorsal laminæ on either side; *e*, chorda dorsalis; *c*, mucous layer of the blastoderma; *d*, vascular lamina, between *b* and *c*, indicated by a finely-dotted line.

twentieth to the twenty-fourth hour, the transparent germinal area is observed to become longer and more fiddle-shaped. The cristæ, or folds of the dorsal laminæ, where they run closest together, appear somewhat sinuously bent (fig. XXXIII. *b*, *b*); here, too, in the pectoral region, on both sides of the dorsal laminæ, near their cristæ, there appear dark, four-cornered looking plates, the future vertebral arches (fig. XXXIII. *c*, *c*, fig. XXXIV. *A*, *f*), which form at first but three or four pairs; the cristæ of the dorsal laminæ are observed to approximate more and more, in order to close and complete the vertebral canal (fig. XXXIV. *A*, over the chorda dorsalis, *e*). Anteriorly they separate to a greater extent from each

FIG. XXXII.

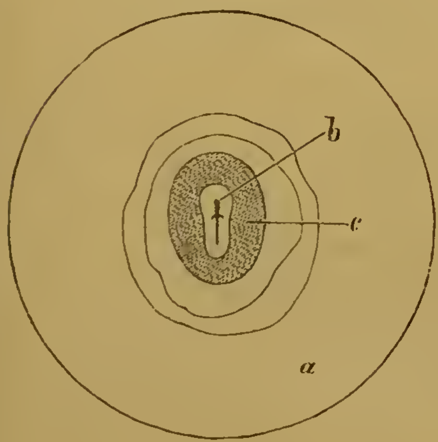

Fig. XXXII.—Vitellus of the natural size after twenty-four hours of incubation, the germinal membrane with the rudiments of the embryo farther advanced than in fig. XXIX. The references are the same in this as in that figure.

FIG. XXXIII.

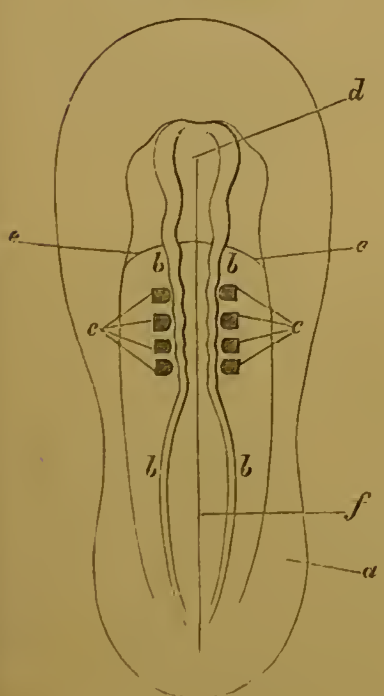

Fig. XXXIII.—Magnified view of the pellucid area of the yolk, fig. XXXII; the area has now lost its pear-shape in a great degree, and become somewhat fiddle-shaped (biscuit-shaped in the original). In the middle are seen the slightly sinuous edges of the dorsal lamina, *b*, *b*, separating from one another anteriorly and posteriorly; on their outsides lie four square plates, *c*, *c*, rudiments of the vertebral column; *d*, anterior cerebral cell; *e*, *e*, transparent edge of the cranial involucrum, shining through; *f*, dorsal cord.

other to form the head (fig. XXXIII. *d*), and also posteriorly to form the future sacrum; the enveloping fold, the future involucrum capitis, is thrown farther back (fig. XXXIII. *e*, *e*); the vascular and mucous laminæ of the germinal membrane follow this bending in (fig. XXXIV. *f*), by which the beginning of the intestinal canal is produced, which as yet is nothing more than a depression on the vitelline side of the serous lamina of the germinal membrane. The embryo lies like a flat-bottomed boat turned over upon the germinal membrane (fig. XXXIV. *B*); the head is already strongly indicated (fig. XXXIV. *B*, *e*)[117].

§ 52. With the second day of incubation the embryo disconnects itself ever more and more from the germinal membrane and the yolk, and rises more distinctly over the germinal area. This takes place by the anterior plait or fold (*involucrum capitis*), con-

[117] Baer views several of the appearances otherwise than as they are described in the text. According to him the brain and spinal marrow are wanting upon the closure of the dorsal laminæ; they would appear to be actually present, however, only in a perfectly transparent and fluid condition; they seem to arise out of a metamorphosis of the nota primitiva. The chorda dorsalis with its sheath is only to be well observed on a transverse section (figs. XXVIII. XXXI. XXXIV. *A*, *e*), and not by viewing the germinal membrane from above, when it only presents itself as a simple streak (figs. XXXIII. and XXXVI. *f*), as if it were the ideal axis of the vertebral column. It disappears completely with the development of the bodies of the vertebræ. In figure XXXIII. the sinuous crumpling and the distance of the cristæ of the dorsal laminæ, are more strongly expressed than they appear without any preparation; the germinal membrane had been here examined under the surface of warm water, by which the particulars mentioned came out in stronger relief. Baer believes that the nota primitiva divides shortly after its formation into two lateral halves—the dorsal laminæ, and a middle streak—the dorsal chorda, a view in which I cannot agree with him.

Fig. XXXIV.

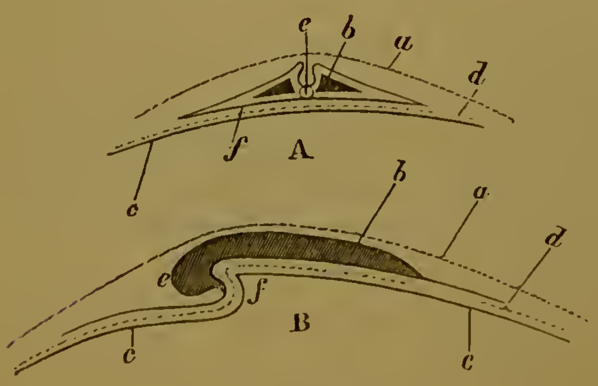

Fig. XXXIV. — Ideal sections of fig. XXXIII. — *A*, transverse section; *B*, longitudinal section. In *A*. *f*, section of the vertebral laminæ. In *B*, formation of the head by the reflexion of the blastoderma; *e*, margin of the involucrum capitis, and entrance into the future intestinal canal (fovea cardiaca of Wolff). The other references are the same as in fig. XXXI.

tinuing to recede still farther backwards (fig. XXXVI. *e*), and the development posteriorly of a second plait or fold, sickle-shaped or

Fig. XXXV.

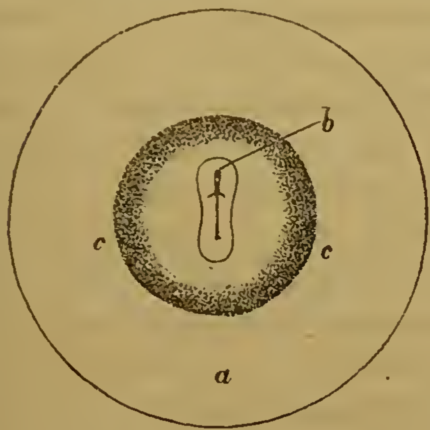

Fig. XXXV. — Yolk of the natural size after thirty-six hours of incubation: *a*, yolk; *b*, fiddle-shaped pellucid area, in the middle of which the embryo is seen. In the vascular area, *c*, *c*, the insulæ sanguinis, or blood islets, begin to appear.

Fig. XXXVI.

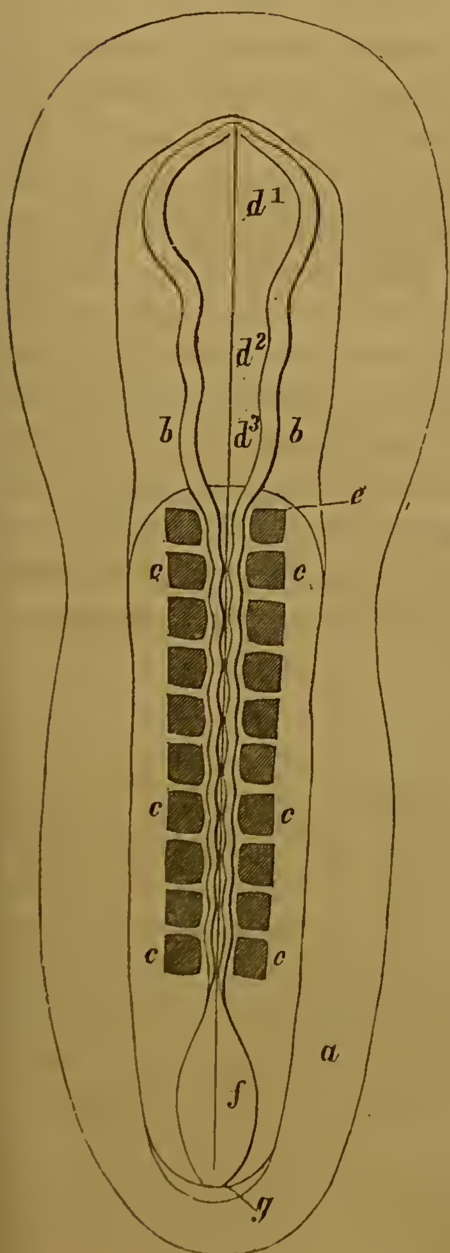

Fig. XXXVI.—Magnified view of the area pellucida of the vitellus, fig. XXXI. —*b*, *b*, crests of the dorsal laminæ, receding from each other anteriorly to form the cerebral cells; d^1, cell of the eyes and thalami; d^2, cell of the corpora quadrigemina; d^3, cell of the medulla oblongata; *c*, *c*, *c*, *c*, laminæ dorsales, of which ten are present on either side; *e*, anterior fold of the blastoderma, from which the involucrum capitis is formed, shining through; *g*, posterior fold of the blastoderma, still very narrow, from which is formed the involucrum caudæ; *f*, chorda dorsalis.

crescentic in the first instance also (fig. XXXVI. *g*), the future *involucrum caudæ;* the sides now begin to turn inwards also, by which the transparent germinal area is drawn in and bent laterally, and made to assume a complete fiddle shape. (figs. XXXV. and XXXVI.) The embryo is three lines in length; the broader and more strongly bent extremity, with its transverse plait or envelope, is visible to the naked eye. The cristæ of the dorsal laminæ have become approximated through a larger space, touch each other (fig. XXXVI. *b*, *b*,) and finally coalescing completely, close the canal for the spinal cord (fig. XXXVII. *A*, *g*), beneath which the more delicate chorda dorsalis with its sheath (*e*), extends. The four-cornered laminæ, the future vertebral arches, have increased in number, new ones springing up in front and behind; and, about the thirty-sixth hour, as many as from ten to twelve pairs may be reckoned (fig. XXXVI. *c*, *c*, *c*, *c*). At this time the dorsal laminæ separate still more from one another in front, so that many spaces or cells become distinctly visible between them; the largest, or most anterior of these cells (fig. XXXVI. d^1) has become somewhat pointed forwards, and curved underneath; laterally it presents wide bending inlets, which indicate the first formation of the eyes; it is the cell of the thalami and crura of the cerebrum; the second smaller cell (d^2), is the cell of the corpora quadrigemina; the third, an elongated cell (d^3) belongs to the medulla oblongata. The transparent mass of the brain and spinal marrow acquires greater consistency, and is covered with a firmer, but highly transparent layer, the future membranous involucra of the nervous centres; the brain, and medulla oblongata, up to this time, are, therefore, in fact, shut vesicles, which, on account of their transparency only, appear as

Fig. XXXVII.

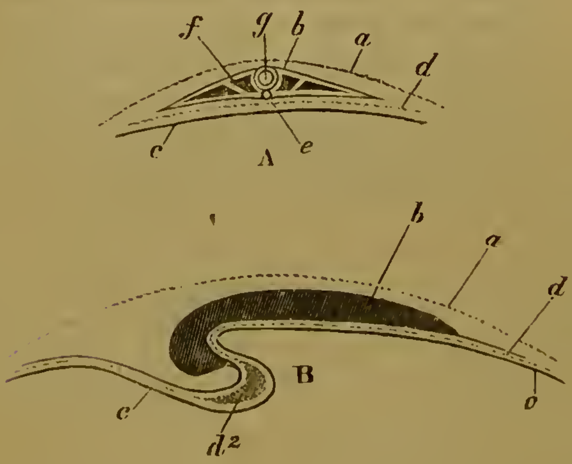

Fig. XXXVII.—Ideal sections of the embryo of fig. XXXII; letters of reference as in fig XXXI. *A* Over the chorda dorsalis, *e*, is seen *g*, the canal for the spinal cord, formed by the union of the cristæ of the dorsal laminæ. *B*, longitudinal section. The heart, d^2, is evolved as a thickening of the lamina vasculosa.

open spaces lying between the sinuous cristæ of the dorsal laminæ. Outwardly, from the cristæ of the dorsal laminæ, and the four-cornered laminæ of the vertebral archcs, proceeds the serous lamina of the germinal membrane, thickening as it grows, and bending from both sides at the same time slightly inwards; in this part a number of small dark folioli or leaflets, make their appearance simultaneously, which become particularly plain in the transverse section (fig. XXXVII. *A*, and especially fig. XL. *A*, b^2); these are the rudiments of the transverse processes of the vertebræ, and, farther out, of the ribs likewise; these lateral prolongations of the serous lamina are called the *laminæ ventrales*, ventral laminæ (*fasciæ abdominales*, Wolff, *laminæ viscerales s. abdominales* of others.) As the dorsal laminæ arise more perpendicularly in plaits, and converge to close the spinal canal, so the ventral laminæ spread more in breadth, bend in inferiorly, and converge to form the lateral parietes of the abdomen, and finally to close this cavity. The vascular and mucous layers follow the turnings and general course of the serous layer, and decline anteriorly under the head of the embryo, by which the *fovea cardiaca* of Wolff, the anterior depression which marks the commencement of the intestinal canal, becomes deeper (fig. XXXIV. *B*, *f*, and XXXVII. *B*). From this sinus the vascular and mucous layers turn more posteriorly, and immediately again proceed forwards, to be continued in the plane of the germinal membrane (fig. XXXVII. *B*, where the heart, d^2, is indicated). This part of the germinal membrane, then, covers the head of the embryo when it is viewed from below, and on this account is called the *involucrum capitis*—the cranial envelope or cap—among writers on development; it is not any independent formation.

Whilst these changes in the form of the serous layer are going on, others are proceeding, pari passu, in the vascular lamina, in the following order, from the end of the first day to the middle of the second. The *area vasculosa* (figs. XXXII. and XXXV. *c*) has enlarged, and from a form rather elongated, has assumed one that is rounder. Its outer circumference is beset with darker aggregated-looking masses (fig. XXXV.); single isolated points appear, and between these clefts are formed, that by-and-by run together and form channels which unite in meshes with one another; in these channels a clear colourless or extremely pale yellow fluid can by-and-by be distinguished in motion—this is the blood. The halones (fig. XXXII.), which had become more sinuous towards the beginning of the second day, now vanish entirely. Along with

these occurrences in the periphery of the vascular lamina, the *development of the heart* has been advancing in the centre, under the transparent germinal area and the serous layer of the embryo. The vascular lamina becomes thicker, and appears darker in this point; the heart shows itself as a somewhat sinuous sac, interposed between and pushing apart the mucous and serous laminæ (fig. XXXVII. *B*, d^2). As the development advances, the heart is observed from the under or abdominal aspect of the

Fig. XXXVIII.

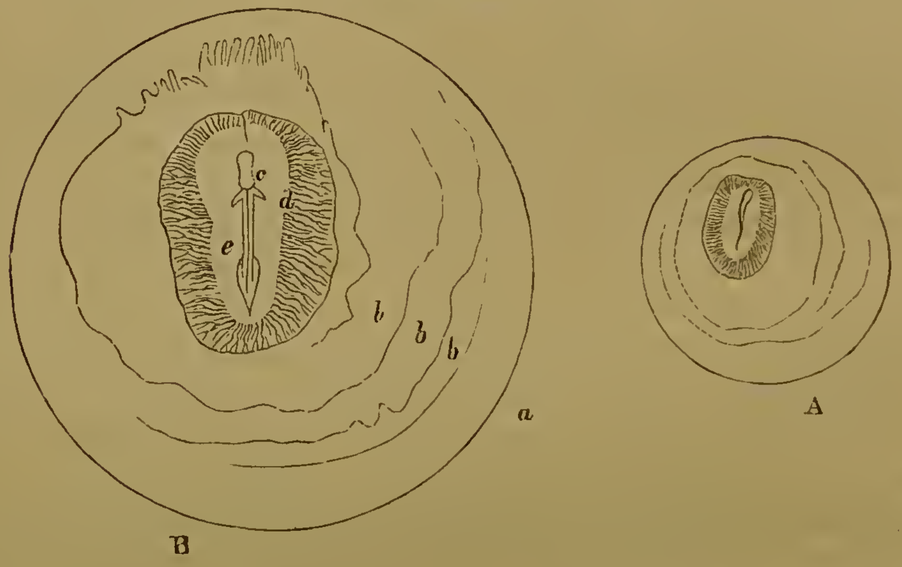

Fig. XXXVIII.—An incubated vitellus of the Jackdaw's egg: *A*, of the natural size; *B*, magnified—*a*, vitellary membrane; *b, b, b*, halones; *c*, embryo; *d*, area pellucida; *e*, area vasculosa. (Compare with figs. XXXII. and XXXV.)

Fig. XXXIX.

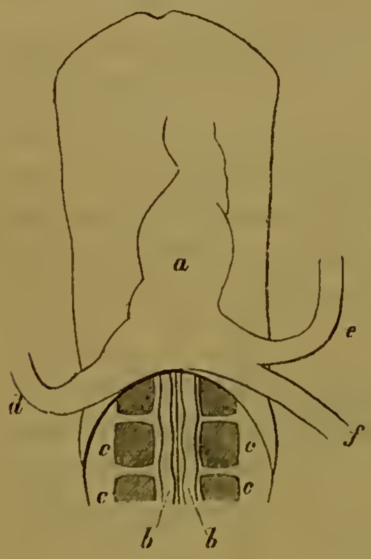

Fig. XXXIX.—Anterior end of an embryo scarcely of greater age than that of fig. XXXII. seen from the abdominal (the vitellary) aspect, to show the first formation of the sacculate heart, *a*, with its immerging vascular (venous) trunks, *d, e, f*; *b, b*, crests of the laminæ dorsales seen shining through.

embryo as a sac, simple and undefined anteriorly, of greater breadth posteriorly, and terminating in two (fig. XXXIX. *d*, *f*) or three (fig. XXXIX. *e*) crura; these are the future great *venous trunks*, which as yet are lost insensibly in the germinal membrane. Even at this period undulating motions, rhythmical contractions of the heart may be perceived, by which the somewhat wavy appearance of the organ is produced; the same clear, or nearly colourless fluid is in motion in the heart as in the vessels in the periphery. The heart occupies the whole space from the involucral point of the germinal membrane to the cranial end of the embryo, and is consequently, when the embryo is contemplated from below, covered by the part of the serous membrane which at the same time forms the involucrum capitis. The embryo, which at the end of the first day bore some resemblance to a punt or flat-bottomed boat, by the middle of the second day has acquired the form of an ordinary small boat turned over, the sides of which (the ventral laminæ) converge, whilst the head is much curved or beak-fashioned (the bending down of the head), and furnished with a particular cover (the involucrum capitis); the posterior part is also somewhat recurved, but much less so than the anterior part, by the commencing development of the caudal envelope. The ventral channel extends from the posterior margin of the heart (fig. XXXIX.) to the crescentic plait of the caudal envelope (fig. XXXVI. from *e* to *g*, seen through the back of the embryo [118]).

[118] The study of these metamorphoses of the first half of the second day is attended with extraordinary difficulties, particularly as regards the first appearance of the vascular system. On the structural changes of the vascular lamina, the formation of the globules of the blood, &c. see Chapter III. in which the several histological metamorphoses are described. [This fundamental idea of the formation of the embryo mediately from a blastoderma, dividing into two laminæ, called serous and mucous, having relation severally, the first to the animal, the second to the vegetative system, has just been called in question by Reichert, in a work of the very highest interest, entitled *Das Entwickelungsleben im Wirbelthierreich*, (*Formative-life in the Vertebrate-Animal-Kingdom*) 4to. Berlin, 1840, which may be regarded as another of the fruits of the discovery of Schleiden and Schwann, of the origin from cells, and mode of elementary formation of organized beings generally. Reichert starts with the principle that the yolk is to be regarded in some sort as the *embryo in a state of solution*, and that the process of evolution does not necessarily take place through the medium of what is called a germinal membrane divided into strata, but immediately from the vitelline matter itself. His researches lead him to conclude that the evolution of the vitellus into the embryo of the vertebrate animal, proceeds according to one of two principles: in the first, which obtains among fishes and the naked amphibia, the central organs of the animal life,—the central nervous and

§ 53. The changes that occur during the second half of the second day, from the thirty-sixth to the fiftieth hour, are the following: the dorsal laminæ are closed along the whole line of their course; the head curves itself more and more under the body, so also does the tail; and the involucra both of the head and tail again bend towards the dorsal aspect; the ocular sinuses are separated more distinctly from the anterior cerebral cell, which now lies completely underneath; the cell of the corpora quadrigemina is much enlarged; from the cell of the medulla oblongata the organ of hearing arises as a vesicular eminence, and in its anterior part, a particular contraction for the cerebellum is very commonly to be perceived; the spinal cord is now a laterally compressed tube. The blood collects in the periphery of the vascular lamina within a circular sinus or annular vessel, the future *sinus s. vena terminalis*. The heart soon parts the ventral laminæ from one another, like a wedge, and so forms a hernia behind the point of reflection of the germinal membrane to the cranial involucrum; it is here that the venous trunks penetrate which carry the blood from the periphery of the vascular lamina to the heart. The heart itself has now become a relatively narrower, and more curved or spirally twisted sac, which contracts with greater vigour than heretofore. The anterior extremity of the heart divides into two crura, which proceed to the cover of the future oral cavity, and run for a certain way under the vertebral column, where they blend into the future aorta, separate again, and give off two great transverse branches, which lose themselves in the germinal membrane towards the periphery of the vascular area. The blood by degrees

mucous systems, as also the allied assisting systems and organs (the skin, the vertebræ, the blood) are severally produced, without intermedium from the vitellus; in the second, which obtains universally among the higher vertebrata, the scaly amphibia, birds, mammalia and man, the immediate evolution of the embryo from the yolk takes place only in reference to the central systems; the part which he names *membrana intermedia* (area vasculosa, formation of the blood) now becomes the mediate instrument by which the further evolution of the embryo from the yolk is carried on. The ovum of the frog (*Rana esculenta* and *R. temporaria*, afforded the ova employed by Reichert) is the best subject for observing the genesis of the embryo immediately from the vitelline matter.—R. W.]

acquires a red colour. The transparent germinal area continues fiddle shaped. In the periphery the serous lamina recedes still more from the other laminæ of the germinal membrane that lie under it, at the same time that it is raised round the whole circumference into a fold which grows with great rapidity in the beginning of the third day (fig. XL. *A*, *B*, *f*). The whole embryo is still more bent on itself; the cell of the corpora quadrigemina forms its anterior and superior end; the caudal end is turned in more than ever, and the mucous layer following the bending, a depression is here formed in the same way as we have seen one produced towards the anterior extremity, at the fovea cardiaca; the digestive cavity is now a channel of considerable depth; which, however, is still largely patulous towards the vitellus, from which undoubtedly it derives formative materials.

§ 54. *Second period of the Development of the Chick, to the evolution of the second circulation.*

The second period in the history of the development of the chick begins with the third day, in the course of which the circula-

Fig. XL.

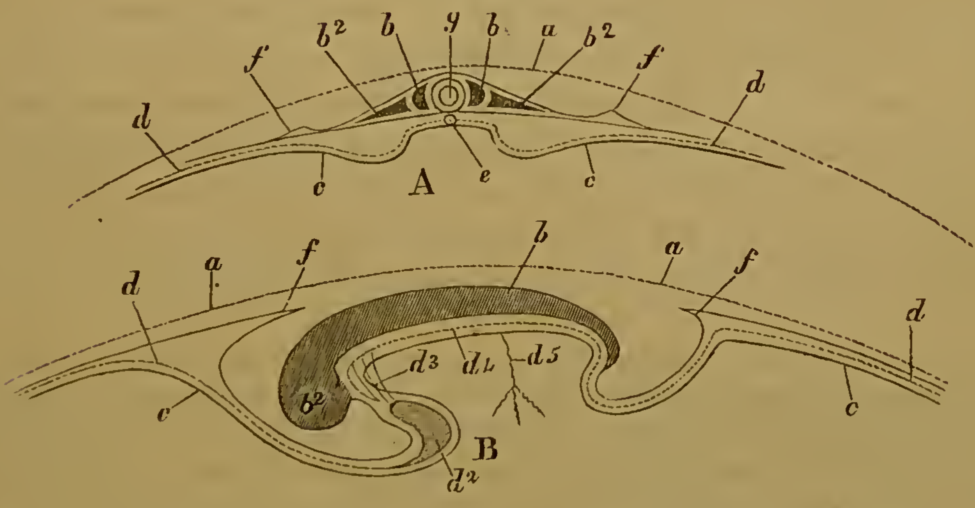

Fig. XL.—Ideal section of an embryo somewhat younger than that of Fig. XLI. *A*, transverse section; *a*, vitelline membrane; *b*, *b*, laminæ dorsales et vertebrales; *b* ², *b* ², laminæ abdominales and transverse processes; *c*, *c*, lamina mucosa, which is seen bending round under the chorda dorsalis (*e*), to form the intestinal canal; *d*, *d*, lamina vasculosa; *f*, *f*, peripheral portion of the lamina serosa, proceeding to form the lateral involucra and the amnion; *g*, medulla spinalis.—*B*, longitudinal section; *a*, vitellary membrane; *b*, lamina serosa, and dorsum of the embryo; *b* ², head of the embryo; *c*, *c*, lamina mucosa; *d*, lamina vasculosa; *d* ², heart; *d* ³, branchial arteries; *d* ⁴, aorta; *d* ⁵, artery of the blastoderma (*arteria vitellina*).

tion in the vitelline vessels is completely established (figs. XLI. and XLVIII.), and embraces farther the changes that take place during the fourth and fifth days, till the allantois has appeared, the membrane of the shell has been attained, and the second circulation is established; the first, which had reached its highest development at the end of the fourth day, now beginning to suffer an arrest, and to decline in extent and activity (figs. XLIII. and XLVII.). In the course of this period the embryo is completely detached from the germinal membrane, and becomes enveloped in peripheral productions of the same part. The third day is the most remarkable in the whole history of the development, as, from the general vigour of the formative processes, all the organs now begin to be evolved, and the characteristic form of the embryo to be more particularly declared. We shall speak of the different appearances in groups, as they are associated with the several laminæ of the germinal membrane, tracing each principal formation, and each individual organ in its progress from the beginning to the end of the period we are now considering [119].

§ 55. The dorsal laminæ have increased in size, and the rudiments of the vertebræ within them (the vertebral laminæ) are growing both anteriorly and posteriorly (fig. XLI. *h*, *h*); they surround the spinal canal on the sides, are also to be seen over the medulla oblongata, and several even exist anterior to the ear (fig. XLII. at *d*) [120]. In the vicinity of the chorda dorsalis, outwardly, between it and the vertebral laminæ, arise the first cartilaginous rudiments of the bodies of the vertebræ, which blend superiorly with the laminæ of the vertebral arches, close in the canal of the spinal marrow below, and surround the cartilaginous column

[119] It may be as well to observe in this place, that the assumption of determinate periods and days has always something arbitrary in it, inasmuch as different eggs advance in their development with very different degrees of rapidity, even when they are kept together in a perfectly equable temperature. Neither do the individual organs always bear the same precise relations to one another in the degrees of their development at the same particular moment: one often appears to lag a little behind another. [The idea of the embryo becoming *pinched off* from the blastoderma, is combated by Reichert (l. c. p. 110).—"The embryo," says he, "does not detach itself from a germinal membrane that to the senses has no existence; neither does it part from the yolk, from which it is to receive development. The supposed pinching off depends much rather on the canalicular formation of the inferior visceral tube and the intestinal system which it includes." —R. W.]

[120] It is usual at this time to observe two pairs of vertebræ lying over the auditory vesicle, as in fig. XLII. *d*.

(sheath) of the chorda dorsalis. Towards the fifth day the chorda dorsalis begins to disappear. The spinal marrow is laterally compressed, and falls into two halves, each of which is again divided into an upper and an under fasciculus. It is on the fifth day that the rudimentary enlargements or processes indicative of the position of the future *extremities,* make their appearance; the earliest traces of the cerebral envelopes were already con-

Fig. XLI.

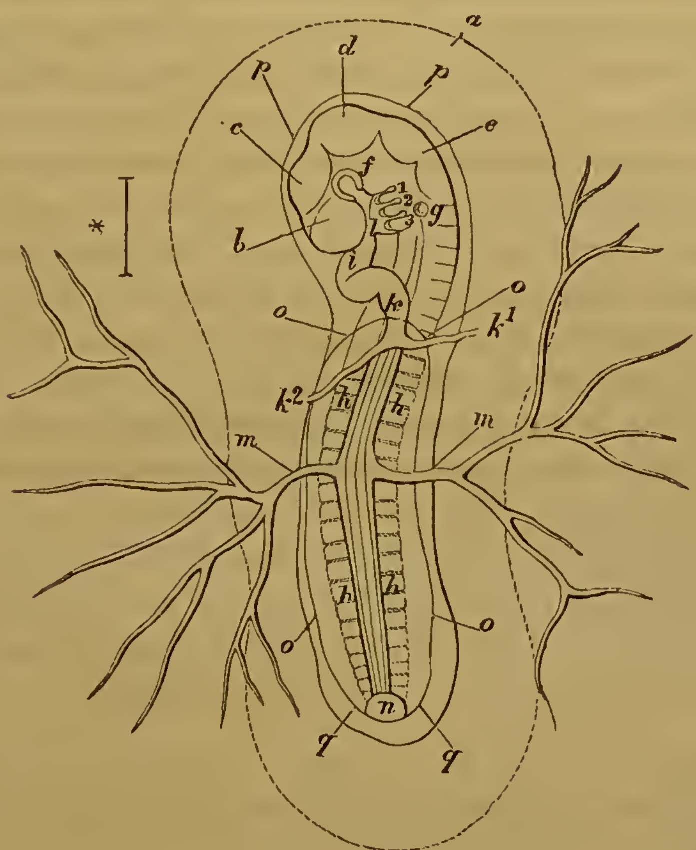

Fig. XLI.—View of an embryo, four lines long, magnified about eight diameters. The embryo is seen from the abdominal surface; the time is the middle of the third day.—*a,* Area pellucida; *b,* anterior cerebral cell (the hemispheres); *c,* cell of the thalami and crura cerebri; *d,* corpora quadrigemina; *e,* cerebellum and medulla oblongata; *f,* the eye, a wide cleft inferiorly; *g,* the auditory vesicle lying in front of the medulla oblongata; *h, h, h,* vertebral lamina; *i,* ventricle of the heart; *k,* atrium cordis; *k* ¹, superior, and *k* ², inferior vein of the blastoderma; *l,* bulb of the aorta, giving off the four branchial arteries, over which lie three branchial arches, 1, 2, 3; *m, m,* arteries of the blastoderma proceeding from the divided trunk of the aorta; inwards from either aorta the bodies of the vertebral laminæ are united by suture; *n,* the Allantois just budding forth; *o, o, o, o,* margins of the abdominal cavity, reflected superiorly into the involucrum capitis, *p*; inferiorly into the involucrum caudæ, *q, q.* The mesentery, Wolffian bodies, &c. which have by this time begun to appear, are left out. The actual length of the embryo is indicated by the line with the asterisk.

spicuous on the fourth day. The medulla oblongata (fig. XLII. between *c* and *d*) is extremely flat above, in consequence of the divergence of the superior fasciculi from one another, and thus is the basis laid of the fourth ventricle, which appears to be covered with its own peculiar medullary and enveloping lamina [121]. Anteriorly, the fasciculi of the medulla oblongata ascend towards the corpora quadrigemina in two perpendicular laminæ, which, on the fifth day, become applied to one another, and so cover the fourth ventricle superiorly and anteriorly; thus is the *cerebellum* produced, visible from the side as an enlargement (fig. XLI. *e*, fig. XLII. *d*, figs. XLIII. and XLVII. a^2), behind which the fourth ventricle presents itself as a deep depression (fig. XLIII. and XLVII. *d*). The *corpora quadrigemina* form a simple and very considerable cell, which projects forwards in an arched or vaulted manner, but, with the increasing declension of the head, turns always more and more downwards (fig. XLI. and XLIX. *d*, fig. XLII. *e*, figs. XLIII. and XLVII. *a*, fig. XLV. *B*, *a*, fig. XLIV. *b*, fig. XLVI. *c*). The laminæ, which form the cerebellum, proceed upwards, blending in the corpora quadrigemina, under which the fourth ventricle is continued as the aqueductus. Anteriorly to the corpora quadrigemina lies the asymmetrical, smaller, middle cerebral cell (figs. XLI. and XLVII. *c*, figs. XLII. and XLIII. *f*, fig. XLV. *B* before *r*), formed by the advancing laminæ of the medulla oblongata as the *crura cerebri;* it is open superiorly, and extends, as the third ventricle, with a wide opening into the infun-

121 The investigation of this point is difficult, and I have not been able fully to satisfy myself that the fourth ventricle is covered with an enveloping layer; the outer coverings over this part are thick, and obscure the view of what lies under them

Fig. XLII.

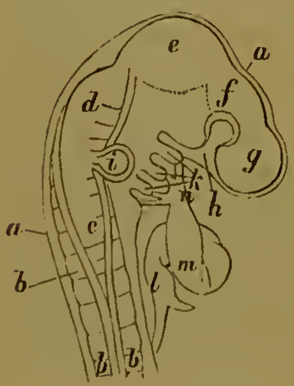

Fig. XLII.—Anterior end of an embryo somewhat more highly magnified and a few hours older than that of fig. XLI. *a*, *a*, Cranial involucrum; *b*, *b*, vertebral laminæ near the crests of the now closed dorsal laminæ; *c*, spinal cord passing into the medulla oblongata *d*, which in its turn passes by a depression (the fourth ventricle) into the corpora quadrigemina *e*; *f*, mesocephalon (thalami and crura cerebri); *g*, hemispheres; *h*, superior maxillary bone; *i*, auditory vesicle; *k*, branchial arches; *l*, atrium cordis; *m*, the heart hanging forwards; *n*, bulb of the aorta.

dibulum, which on the second day was directed straight downwards, but which now, from the great bending in of the head, is turned backwards, and even upwards. In this cell, which was the first formed, and foremost cerebral cell (fig. XXII. d^1), the *thalami* make their appearance towards the end of the period. The most anterior cerebral cell at the present epoch is symmetrical, and contains the hemispheres (figs. XLI. XLII. XLIII. and XLVII. *b*, fig. XLII. *g*, fig. XLVI. *d*, fig. XLV. *B*, *p*); according to the natural curvature of the embryo, it lies completely downwards. The *optic nerve* appears as a vesicle betwixt the middle and anterior cerebral cell, in which the external envelopes (the outer portion of the serous membrane), preparatory to the formation of the *eye ball*, bend circularly inwards in the shape of a sac, and externally form a projection, which opens downwards as a cleft; this is closed by degrees, and at length forms a colourless thin streak, whilst the rest of the bulb, from the deposition of the pigmentum nigrum, is dark or deeply coloured; the *lens* makes its appearance very early (on the third day), forming a particular closed capsule within the sac of the external envelopes (the ball of the eye), and lying in the midst of an albuminous ball, the *vitreous humour*. (On the meta-

[122] The development of the eye is among the most difficult points in the whole subject; much remains to be done in it. The labours of Huschke upon the point are admirable. Vide Meckel's *Archiv für* 1832, S. 1. tab. i, and Ammon's *Zeitschrift für Ophthalmologie*, B. IV. S. 272, tab. ii.

Fig. XLIII.

Fig. XLIII.—Embryo of the fowl, nearly five lines in length, at the seventy-second hour of incubation (transition from the third to the fourth day). The abdominal surface is partly laid open and the parts separated; the amnion is removed. *a*, Corpora quadrigemina; *b*, the hemispheres; *c*, the nasal depression; *d*, the fourth ventricle, in front of which lies the cerebellum a^2, which is now more distinctly defined; *e*, the ear; *f*, the eye, in the choroid of which, already furnished with its pigment, a cleft is seen; g^1—g^4, the four branchial clefts; *h*, the heart; *i*, the liver; *k*, the intestinal canal, with its open vitellary duct *l*; *m*, the rectum still ending in a blind sac; *n*, the allantois; *o*, the anterior, and *p*, the posterior, extremity; *q*, *q*, *q*, *q*, Wolffian bodies; *r*, upper jaw; *s*, under jaw.

morphosis of the eye, consult figs. from XLI. to XLII). The *organ of hearing*, at first a simple vesicle arising from the medulla oblongata, soon becomes a distinct sac, which, examined from behind, appears attached to the medulla oblongata by means of a pedicle,—the *acoustic nerve* (fig. XLII. *i*); distinct from it a cleft appears (fig. XLIV. *A, f*), which increases over against the acoustic sac, and sinking into it, forms the external *meatus auditorius*. If the embryo be lying upon its side, the acoustic sac, which subsequently forms the labyrinth, is seen as a rounded enlargement (fig. XLI. *g*, XLIII. *e*, XLIV. *A, n*), which in the course of the period under consideration comes continually forward. About the

Fig. XLIV.

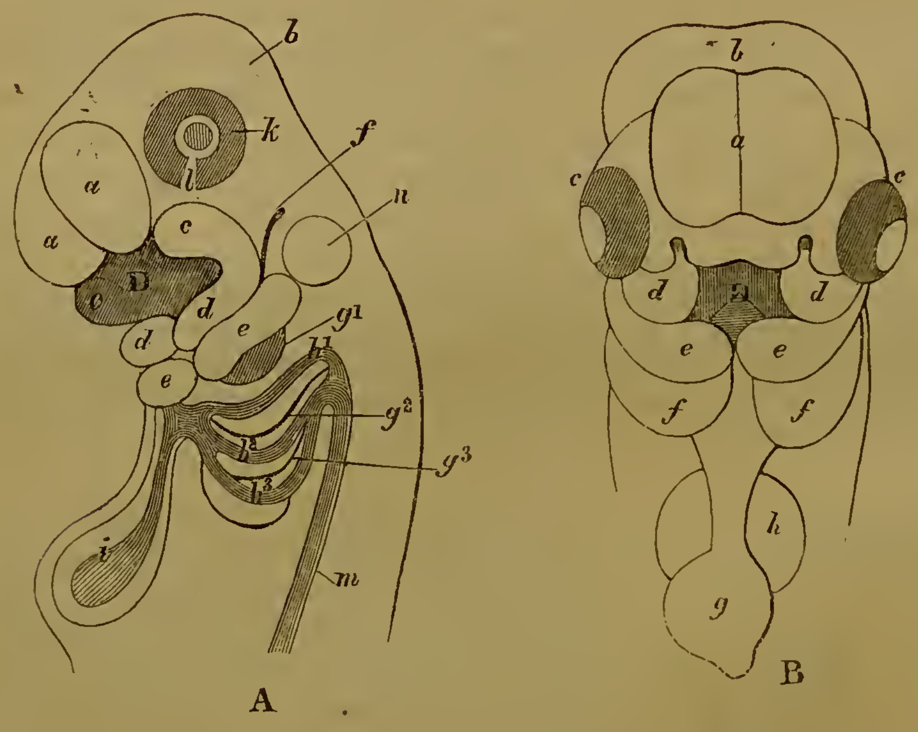

Fig. XLIV. *A*.—Embryo of the fowl of the fifth day, much magnified; after Huschke (*Isis*, 1828, § 163.)—*a, a*, hemispheres; *b*, corpora quadrigemina; *c*, upper jaw; *d*, under jaw; *e*, first branchial arch (*os hyoïdes*); *f*, meatus auditorius externus; g^1, g^2, g^3, first, second, and third branchial fissures; h^1, h^2, h^3, the three branchial arteries; *i*, the heart; *k*, the eye with the cleft *l*; *m*, descending aorta; *D*, cavity of the mouth and fauces; *n*, acoustic pouch.

Fig. XLIV. *B* (after Huschke), front view of the embryo of the fowl, of the fourth day: *a*, hemispheres; *b*, corpora quadrigemina; *c*, eye; *d*, upper jaw; *e*, lower jaw; *f*, enlargement of the os hyoides; *g*, ventricle of the heart; *h*, atrium cordis; *D*, oral aperture and faucial cavity.

beginning of the third day, the *olfactory nerve* shows itself towards the basis of the cell of the hemispheres; at a later period the *nasal hollow* (fig. XLIII. *c*) is observed as a broad depression with puffed edges; on the fifth day both nasal hollows have become deeper, and are now distinct from one another.

§ 56. Very important metamorphoses go on during this period in the ventral laminæ lying on either side of the dorsal laminæ, or middle portion of the embryo; so far these ventral laminæ are formed from the serous layer of the germinal membrane only; they separate into a superficial thinner layer (figs. XL. and XLV. *A*, b^2 and *f*), which, like a cuticle, loses itself in the peri-

Fig. XLV.

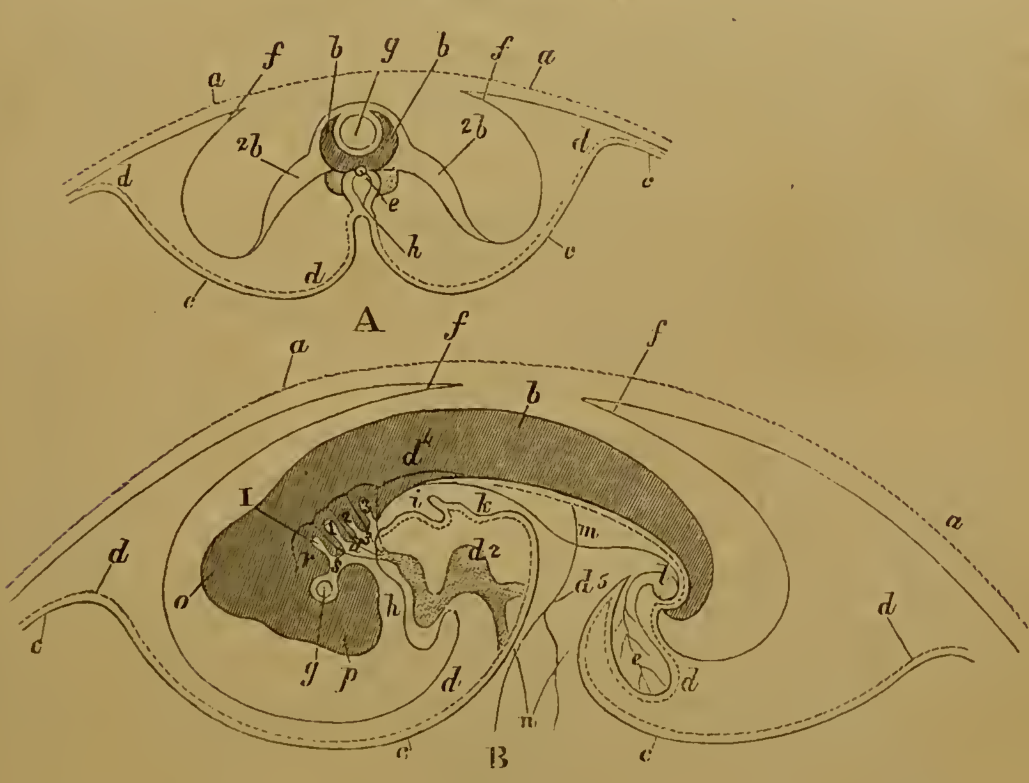

Fig. XLV.—Ideal section of an embryo nearly at the end of the third day:—*A*, transverse section; *a*, vitelline membrane, *b*, *b*, laminæ dorsales, &c. as in fig. XL. *B*, longitudinal section. The cranial and caudal involucra approximate, and at length meeting, they close the amnion; *g*, the eye; *h*, entrance into the mouth, or fovea cardiaca; *i*, the œsophagus, with the rudimentary lung budding out as a diverticulum from it; *k*, expansion of the alimentary tract, marking the seat of the stomach; *l*, posterior shut extremity of the intestine, from which proceeds the allantois *e*, surrounded by the vascular lamina *d*; *m*, the mesenteric lamina; *n*, passage from the vitellus to the open abdomen; *o*, anterior part of the head (corpora quadrigemina); *p*, hemispheres; *r*, superior maxilla; *s*, inferior maxilla; *I*, oral cleft or aperture; 1, 2, 3, three branchial clefts. Other references as in fig. XL.

phery of the embryo upon the deeper stratum; and, as it has already suffered a reflection anteriorly opposite the heart, and formed the involucrum capitis; so, towards the posterior part, it has bent over as the involucrum caudæ, and been formed into plaits or folds laterally, as the lateral envelopes. Thus is the serous layer of the germinal membrane, or upper layer of the ventral laminæ, raised on every side to converge into an elliptical plait towards the back of the embryo; on the fourth day, these plaits have approached each other very closely; the anterior is now called the *vagina capitis* (fig. LXV. *B, f,* forwards); the posterior *vagina caudæ* (fig. XLV. *B, f,* backwards); the lateral folds may, in like manner, be entitled the *vaginæ laterales* (fig. XLV. *A, f, f*); they coalesce at the end of the fourth day, and form a visible cicatrice over the lumbar region of the embryo. In this way we have a complete vesicular envelope thrown around the embryo,—the AMNION, (fig. XLVI. *a, a,*) which is filled with fluid. The

Fig. XLVI.

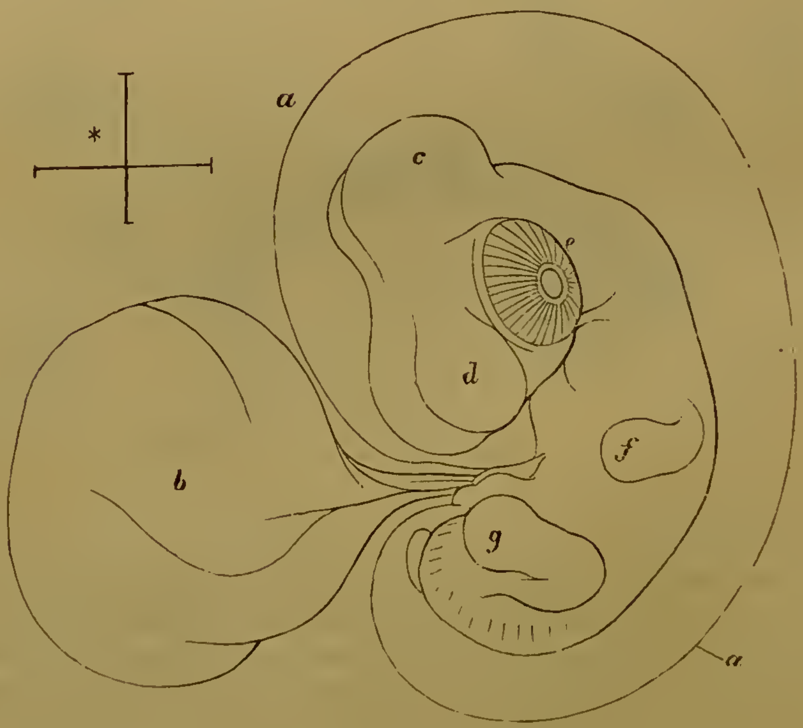

Fig. XLVI.—Outline of the embryo of the fowl, at the end of the fifth day, much magnified; *a, a,* amnion; *b,* allantois; *c,* corpora quadrigemina; *d,* hemispheres; *e,* eye; *f,* anterior, and *g,* posterior extremity. The natural dimensions of this, as of many of the other figures, are indicated by a line or lines with an asterisk.

upper layer of the fold (fig. XLV. *A* and *B*, lying under the vitelline membrane, *a*,) covers the whole germinal membrane, and grows around the yolk as a serous capsule or cyst, *vesica serosa*—the false amnion of Pander. At the place where the embryo lies, this layer is separated from the rest of the germinal membrane by a considerable space. The inferior layer of the serous ventral lamina forms the ventral paries, and gives origin to the bones and muscles which compose the neck and trunk. Inferiorly, the vascular lamina lies upon it, and this, with the serous lamina, evolves the formations which are now to be described. On either side, under the vertebral column, there is a lamina detached, which grows thicker, and increases in a direction perpendicularly downwards; these are the *laminæ mesentericæ*, between which there is, at first, an open triangular-shaped channel or cleft, the *foramen mesenterii* (erroneously regarded by Wolff as an intestinal channel); both the mesenteric laminæ push the mucous layer before them, and speedily unite, at an acute angle, in the suture—*sutura* (fig. XLV. *A*, *h*, *B*, *m*). The furrow or foramen of the mesentery resembles an equilateral triangle, with one of its angles pointing directly downwards. After the union of the two mesenteric laminæ, the resulting structure grows most rapidly posteriorly, opposite the middle of the body, and here forms a septum, dividing the abdominal cavity into two halves.

It is at the beginning of the intestinal canal, where the ventral laminæ are converging, that the *branchial arches* are developed; the parietes of the body here become thinner; and in this, the cervical region, several clefts or fissures make their appearance, which sink downwards, and penetrate through the mucous layer; there are three pairs, or, with the oral aperture, four pairs of such fissures, but the posterior pair are extremely small; they are called the *branchial fissures*—fissuræ branchiales ([123]); between

[123] The discovery and true interpretation of the branchial fissures in the embryo of the higher vertebrata, belongs to Rathke, *Isis*, 1825, vol. i.; *Nova Acta Acad. Natur. Curiosor.* xiv. Shortly after this, Huschke illustrated the matter, particularly in the chick, *Isis*, 1826 and 1827. Very recently Reichert has pursued the subject deeply; he calls the branchial arches *visceral arches*—Müller's *Archiv für* 1837. His assertion, that these are not *branchial* arches, is a mere dispute about a word; it was never imagined that the parts in question were proper *gills;* but they are vascular arches, which are in every respect analogous to the vascular arches of the gills of fishes, only not branching like these.

them lie three segments or divisions of the ventral laminæ, which are blunt and rounded anteriorly, bevelled off towards the digestive cavity, and therefore sickle-shaped; these are named the branchial arches—*arcus branchiales* (figs. XLI. XLII. XLIII. XLV. &c.); the fourth branchial arch is placed hindmost, and is not yet distinct from the ventral lamina. On the fourth day, the two most anterior branchial arches increase in thickness (fig. XLIII. between g^1 and g^2); a new fissure is formed posteriorly (fig. XLVII. g^4); on the fifth day, the foremost fissure closes (fig. XLIV. *A*, between *d* and *e*), and the foremost branchial arch unites with its fellow of the opposite side, and forms the *lower jaw* (fig. XLIV. *A*, *d*, *B*, *e*); the next in succession is transformed into the *os hyoides* (fig. XLIV. *A*, *e*, *B*, *f*). The two last branchial fissures close up on the fifth day; at the same time, the first is lost entirely; but the second continues longer open (fig. XLIV. *A*, g^1)[124]. On the third and fourth days, the part of the ventral lamina, which is situated in front of the lower jaw, thickens and resolves itself into the *upper jaw* (fig. XLIII. *s*, and XLVII. 1, above 2); this part is more strongly marked on the fifth day (XLIV. *A*, *c*). The two sides of the upper jaw do not meet in

[124] The first branchial fissure is metamorphosed internally into the Eustachian tube, externally into the external meatus (fig. XLIV. *A*, *f*). I have, I may state, found that the order in which the branchial fissures disappear is far from being quite regular; the whole of them may, in many cases, be found existing more or less simultaneously (fig. XLVII. &c.).

Fig. XLVII.

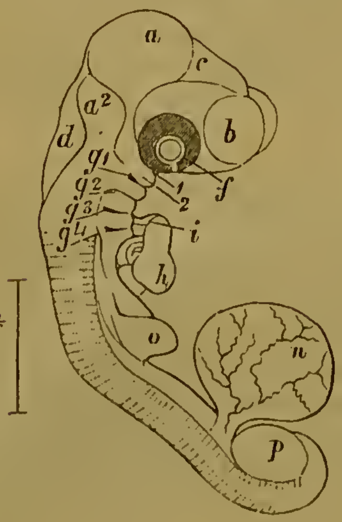

Fig. XLVII.—Embryo of the fowl of the first half of the fourth day; *a*, corpora quadrigemina; *b*, hemispheres; *c*, mesocephalon (thalami); *d*, fourth ventricle; *f*, eye, the cleft in the choroid beginning to close; g^1, g^2, the first and second branchial spaces still entirely open; g^3, g^4, the third and fourth spaces open behind only; *h*, the ventricle of the heart, now of a rounded form; *i*, aorta; *n*, allantois; *o*, anterior, and *p*, posterior extremity. 1, 2, upper and under jaw. The line with the asterisk indicates the natural length of the embryo.

the first instance; they coalesce at a later period, through the medium of the frontal process, which is developed betwixt the eyes (fig. XLIV. *B*, over *D*.)

The rudiments of the *ribs* begin to be formed in the parts of the ventral laminæ which lie behind the branchial arches; the extremities show themselves upon the external aspects of the same laminæ. Of the *extremities* there is still no trace to be discovered in the first half of the third day (fig. XLI.), but in the second half of that day they arise on the sides of the ventral laminæ as narrow edgings, which by the close of the day have turned more upwards, gained the outer margins of the ventral laminæ, and changed into rounded offsets (fig. XLIII. *o, p*), the posterior pair being distinguished from the anterior by somewhat greater breadth (fig. XLVII. *o, p*), on the fifth day they recede still more upwards towards the dorsal laminæ, become pediculated, and present a broad shovel-shaped termination (fig. XLVI. *f, g*).

§ 57. The *vascular lamina* in its development follows the phases of the first, or vitellicular circulation, which, as has been

Fig. XLVIII.

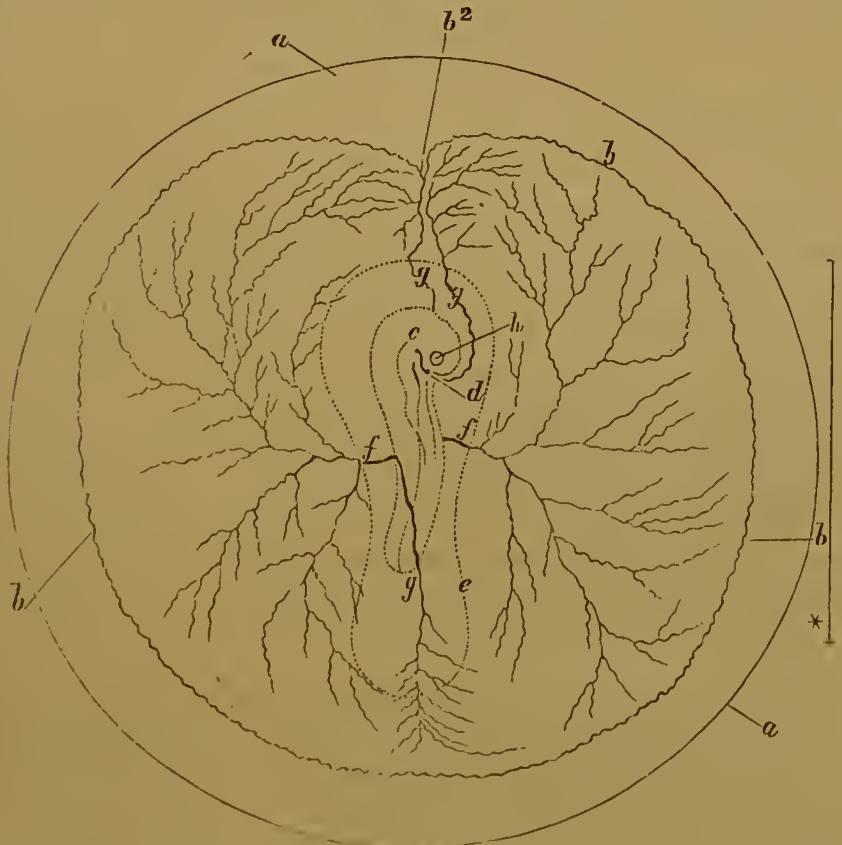

Fig. XLVIII.—View of the Vitellus, magnified rather more than two diameters, exhibiting the circulation of the blastoderma completely developed:—*a*, Vitellus; *b*, vena s. sinus terminalis; b^2 point of approximation to the embryo

stated, attains its height on the fourth day (fig. XLVIII.). Immediately under the head of the embryo, three blood-red bounding points are seen (fig. XLVIII. *d*), the expression of the alternating contractions of the three divisions of the heart, which are now in the course of formation,—the *sinus venosus* (fig. XLI. *k*, XLII. *l*), which receives the veins, and towards the end of the third day shows traces of the two auricles, the *ventricle* (XLI. *i*, XLII. *m*), and the *bulbus aortæ* (XLI. *l*, XLII. *n*), divided from the ventricle by a contraction. In this period the heart presents such diversities that it may be said to be in a state of ceaseless metamorphosis, both as regards form and position. On the second day, it is a somewhat spirally twisted canal lying under the brain (fig. XLI. *i*); on the third day, it has drawn itself more backwards, become more concentrated, and bent round as it were into a kind of loop (fig. XLII. *m*), when it appears to project in the form of a tumour between the ventral laminæ (figs. XLII. and XLIII. *h*), first inclining to the left and then to the right, and being all the while within the compass of the involucrum capitis (fig. XLIX. *f*). The ventricle, which during the third day is still canalicular, becomes more globular on the fourth day (fig. XLVII. *h*), and pointed underneath, so that it acquires the proper heart-shape (fig. XLIV. *B*, *g*); it then lies very much to the right, whilst the sinus venosus, which is become more distinct from it, lies more to the left (fig. XLVII. behind *h*). At the end of the third day, the constriction between the ventricle and aortal bulb (the fretum of Haller), is already well marked (fig. XLII. *n*). On the fourth day, the muscular mass of the heart and the septum ventriculorum is produced; in the sinus venosus the septum is not begun to be formed till the fifth day, and the two apices into which the veins even on the third day were seen to plunge (fig. XLII. below *l*), enlarge, and become the auricles. Some time before the bulbus aortæ becomes distinctly pinched off (fig. XLIX.), it divides at the beginning of the third day into four pairs of vascular arches, which show themselves through the abdominal laminæ, the most posterior of the four

of the terminal sinus, and its communication with the veins *g*, *g*; *c*, aorta; *d*, punctum saliens, or pulsating point of the heart; *f*, *f*, arteries of the blastoderma; *g*, *g*, veins of the same (one inferior, two superior; sometimes there is but one above as well as below); *e*, *e*, the fiddle or guitar-shaped area pellucida; *h*, the eye. (This figure will be found to correspond in almost every particular with that of Pander, tab. iv. fig. 1. of his well-known work, *Entwickelungsgeschichte des Hühnchens im Eie*). The more delicate ramifications of the vessels and their numerous inosculations with the bounding sinus are omitted.

being the smallest (fig. XLIX. 1—4); after the formation of the branchial fissures they lie behind the sickle-shaped branchial arches (figs. XLI. XLV. *B*, XLII.); they unite on either side upon the vertebral column into a radix aortæ, or aortal root; the two aortal roots blend more posteriorly, and form the aorta in common (fig. XLIX.). The vascular arches undergo considerable changes in the course of the fourth day: the first pair gradually disappears and is at length obliterated, and the second becomes smaller; but on either side there is a fifth arch formed, which becomes larger on the fifth day, whilst the second now disappears, so that on this day there are three vascular arches present, all of nearly equal magnitude (fig. XLIV. *A*, h^1, h^2, h^3). The carotid, and by-and-by the vertebral, arteries now make their appearance, arising from the aortal roots, and the bulbus aortæ undergoes a division into two passages. On the fourth day the aorta gives off distinct vessels between the several divisions of the vertebræ; it then divides and furnishes two principal branches, which go off in transverse directions (fig. L. *c*, XLIX. *i*, *i*, XLI. *m*, *m*, XLVIII. *f*, *f*), and splitting into branchlets, form an extremely beautiful network upon the outspread germinal membrane; the aorta afterwards proceeds, first divided and then single, along the vertebral column, gives off a mesenteric artery (fig. XL. XLV. *B*, d^5), and finally splits into two branches that ramify upon the allantois (figs. XLIII. XLVII. *n*). Almost simultaneously with the formation of the arteries an accompanying system of veins is developed; the veins of the germinal membrane, however, are so far in opposition

Fig. XLIX.

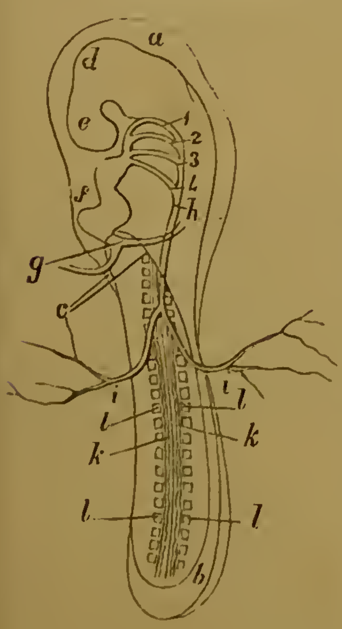

Fig. XLIX.—Embryo of the yolk depicted in fig. L. seen from the abdominal aspect, magnified. *a*, Vagina s. involucrum capitis; *b*, vagina s. involucrum caudæ (*a* and *b*, folds of the germinal membrane enveloping the head and tail); *c*, *c*, anterior passage of the involucrum capitis into the lateral involucra; *d*, vault of the mass appertaining to the corpora quadrigemina; *e*, anterior cerebral mass or lobe; *f*, heart; *g*, termination of the venous trunks in the future atrium cordis; *h*, aorta; 1, 2, 3, 4, the four branchial arteries; *i*, *i*, arteries of the blastoderma; *k*, *k*, translucent crests of the dorsal laminæ, rendered somewhat wavy by the water in which the embryo is immersed; *l*, *l*, vertebral laminæ.

to the arteries, that whilst these are directed transversely towards the sinus terminalis (fig. XLVIII. *f*, *f*), those run parallel with the long axis of the embryo; one inferior, larger vein lying on the left (fig. XLVIII. *g*, XLI. k^2), to which comes a second, smaller, often scarcely perceptible one, situated on the right, and either one or two superior veins (fig. XLVIII. *g*, *g*, XLI. k^1) bringing the blood from the vascular area to the heart. The system of the venæ cavæ is evolved in the body of the embryo at a still earlier period than the arterial system, and the portal system is distinctly separated on the fourth day and ramifying in the liver. The circulation upon the germinal membrane is therefore a vitellicular circulation; the blood courses from the embryo through the two arteriæ vitellinæ *s.* omphalo-mesentericæ (fig. XLVIII. *f*, *f*), to the sinus terminalis or vascular circle, which on the fourth day appears quite full of blood; from this the blood is returned to the heart through the four venous trunks,—the venæ vitellinæ *s.* omphalo-mesentericæ (fig. XLVIII. *g*, *g*, *g*). The smallest arteries and veins also communicate with one another by their most delicate extremities, and form a beautiful rete with rhomboidal-shaped meshes [125].

§ 58. There is a very peculiar formation belonging to the fœtus alone, and having a temporary or transitory character, which must now be mentioned, namely the *Wolffian bodies,—corpora Wolffiana,*

[125] Reichert states that but three branchial vascular arches exist on either side, and that they move gradually more and more backwards, so that the evolution of new arches and the disappearance of older ones are merely apparent. In my earlier researches, I conceived that I saw four vascular branchial arches existing simultaneously in the manner I have figured them; I have never observed five arches, although Baer speaks of them as so numerous.

Fig. L.

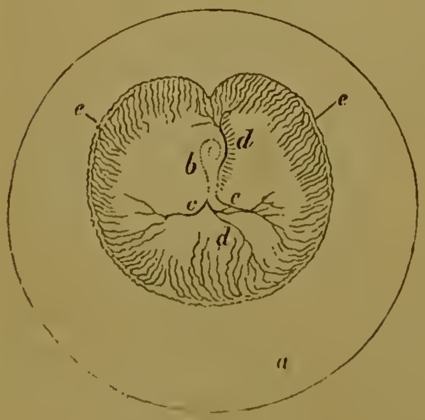

Fig. L.—Yolk of the hen's egg, of the natural size, but flattened through loss of support, at the beginning of the third day of incubation, exhibiting the earliest traces of the circulation.—*a*, Vitellus; *b*, embryo; *c*, *c*, arteries of the blastoderma; *d*, *d*, veins of the blastoderma; *e*, *e*, sinus terminalis.

or primordial kidneys [126]. These bodies are a product of the vascular membrane, though the serous layer would also seem to have some share in their formation. They make their first appearance in the second half of the third day, as a pair of narrow but thick striæ, which sprout outwardly from each mesenteric lamina, in the angle formed between this and the ventral lamina in the line of the vertebral column, from the region of the heart as far as the allantois. Even at this early period they exhibit interchanging elevations and notches, and a canal or duct running in the line of their long axis. On the fourth day the corpora Wolffiana are recognized as being formed out of hollow cœcal-like appendages, which are attached along the course of the duct or canal (fig. XLIII. *q*, *q*, *q*, *q*); on the fifth day they look very broad and thick, and the cœcal appendages are convoluted. The germ-preparing sexual organs, the *testicles* and *ovaria*, make their appearance as delicate striæ on the inner sides of the corpora Wolffiana [127].

§ 59.—The metamorphoses of the mucous layer of the germinal membrane begin, during this period, with the formation of the *intestinal canal.* After the mucous layer, above the involucrum capitis, has struck in under the head, and formed the *anterior access* to the intestinal canal,—*aditus anterior ad intestinum* (Baer), *fovea cardiaca* (Wolff), the same layer also bends in at the opposite extremity, over the involucrum caudæ or caudal envelope, and here forms the posterior access to the intestine, *aditus posterior* (Baer), *foveola inferior* (Wolff); by the increased curvature of the embryo, and the growth of the ventral laminæ, these depressions form funnel-shaped hollows, which terminate, in blind extremities, towards the head and tail. Almost simultaneously with the formation of the branchial fissures, or perhaps a little earlier, the space between the fore end of the head and the heart grows thin, and the mouth and fauces break through, so that a free communication results betwixt the fovea cardiaca and the cavity of the amnion (fig. XLV. *B*, *h*). The intestinum

[126] Casper Frederick Wolff is the discoverer of the bodies which have received their title after him. Vide his *Diss. sistens Theoriam Generationis*, Halæ, 1759. Valentin has given a very complete history of their discovery and development, —*Entwickelungsgeschichte*, p. 235.

[127] The corpora Wolffiana are also described at great length by Müller, in his account of the formation of the genital organs (*Bildungsgeschichte der Genitalien*), where he has also given the most complete view we possess of the development of the sexual organs of birds.

rectum, on the other hand, (the posterior funnel-shaped involution of the mucous layer) continues longer closed. By the formation of the mesenteric laminæ the mucous layer is detached from the ventral laminæ, and pushed downwards (fig. XL. *A*, under *e*); as soon as the mesenteric laminæ have coalesced, the mucous layer also converges from both sides under the mesentery, and where it is accompanied by the prolongations of the vascular lamina, which proceed from the mesenteric laminæ, two new laminæ present themselves, the *intestinal laminæ*,—laminæ intestinales, which run perpendicularly downwards (fig. XLV. *A*, under *h*), and the mucous layer being thus bent inwards in a canalicular manner, forms the *intestinal cleft*,—an open canal in communication with the yolk, running forwards funnel-shaped towards the faucial cavity, and backwards in the same manner to the rectum. At the beginning of the fourth day, the intestinal cleft has contracted, and exhibits but a very small opening, which, extending soon after into a canal or sac (fig. XLIII. *k*, *l*) passes over the peripheral mucous layer as the *intestinal canal* (fig. XLV. *B*, *n*), and throws itself completely around the yolk. The oral and faucial cavity gapes widely, and extends into a narrower part or canal, the œsophagus, from which, inferiorly and posteriorly, a diverticular sacculus sprouts (fig. XLV. *B*, *i*), the first rudimentary appearance of the *lungs;* a little farther on, an elongated enlargement of the intestine is perceived, which indicates the situation of the future *stomach* (fig. XLV. *k*); the intestine then expands, and goes off funnel-shaped towards the yolk (fig. XLV. *n*, and in a later form, fig. XLIII. *k*, *l*), and in like manner towards the rectum, which still terminates in a blind sac; the limits between the small and large intestines are indicated by the evolution of a couple of diverticula,—the *capita cæca*, towards the end of the third day. About the middle of the third day, various other parts are indicated in connexion with the intestinal canal, which enlarges in the places where these are to appear, and sprouts out towards or into the vascular layer; thus, two little hollow off-sets show themselves as the rudiments of the *liver*, in which a venous net-work by and by appears, that resolves itself into the portal system. At the beginning of the fourth day, the two lobes of the liver appear as lappets of some breadth (fig. XLIII. *i*), in which the composition, by means of an aggregation of blind sacs, is apparent somewhat later; another small off-set or hunch also shows itself in the vascular layer, between the lobes of the liver; this is the *pancreas* about to be; it grows slowly, but, on the fifth day, when the *convolutions of the small intestine* begin to

be formed, it has enlarged considerably; at this time, the *spleen* also makes its appearance as a small red body. The pulmonic sac divides, and becomes more distinct, from the œsophagus appearing first pinched off from that part, and then provided with a pedicle,—the future *trachea;* on the fifth or sixth day, the lung of the one side is completely distinct from that of the other, and each is attached to the common pedicle by a particular branch, the future *bronchi;* the pedicle has farther extended, as the *trunk of the trachea.*

In the course of the first half of the third day, a small vesicular-looking protuberance arises from the intestinum rectum (fig. XLI. *n*); this proves to be the *allantois,* which grows into the caudal involucrum, and distends it. The allantois is covered externally with a stratum of the vascular layer (fig. XLV. *B, e, d,*) which it carries with it in its growth. The growth of this part is very rapid in the course of the fourth day (fig. XLIII. XLVII. *n,*) forcing its way through the caudal involucre, and the part by which it is attached being drawn out into a hollow pedicle. The external covering from the vascular layer shows ramifications of the aorta, which form a beautiful vascular rete. On the fifth day, the allantois presents itself as a large pedunculated bladder protruding from the umbilicus (fig. XLVI. *b*), which, bending to the right, has penetrated between the mesenteric and ventral lamina, and lies betwixt the amnion and the serous envelope. At this time, the allantois is nearly as large as the entire embryo (fig. XLVI.), being almost five lines in diameter[128].

§ 60. *Third period in the history of the development of the incubated Egg: From the commencement of the circulation in the allantois to the exclusion of the Embryo.*

The third and last period comprises the interval from the sixth to the twenty-first day. The two first days, however, comprehend almost all of general physiological interest which happens in this period, so that a shorter review of the grand features of the changes which take place in the embryo and ovum through its course will be sufficient. If the egg be opened at the beginning

[128] According to Rathke, the lungs are evolved from the first as a pair; he describes them, on the fourth day of the incubation, as two small, laterally compressed, thin laminæ, tapering off from before backwards, and ending in a blunt point, which spring from the œsophagus; see his paper on the development of the respiratory system in birds and the mammalia (*Ueber die Entwickelung der Athemwerkzeuge, &c*, in *Nov. Act. Acad. Nat. Cur.* vol. xiv. p. 170.) Baer also speaks of the lungs as originating in two hollow sacculi, which lengthen with rapidity into a hollow peduncle, *Entwickelungsgeschichte,* ii. 126.

of this period, it must be done with great care, as the albumen has now entirely disappeared, and the embryo lies close to the membrane of the shell; the vitellary membrane has become exceedingly thin, is very easily torn, and indeed is soon resolved entirely; the air-space at the blunt end of the egg has greatly increased in size. The germinal membrane now extends over the whole of the yolk; or the mucous layer of this part has almost entirely grown around, and so given origin to a sac-like covering, the *vitellary sac* (vitelliculum, or vitellicle, Owen), which encloses the yolk; the vascular layer has grown around nearly two-thirds of the yolk. The sinus terminalis of this layer is now a mere seam in the periphery of the area vasculosa, and in the course of the next few days disappears entirely; the veins, and then the arteries of the vascular layer of the vitellary membrane disappear somewhat later. On the other hand, the allantois is growing with great rapidity, and, on the sixth day, forms a pretty large flattened bladder (fig. LI.) which, however, in the course of the seventh

Fig. LI.

Fig. LI.—Embryo of the fowl with the allantois, *a*, already of great size, and depressed or flattened, the umbilical vessels, *b*, branching over it; *c*, external ear indicated by a depression; *d*, cerebellum; *e*, corpora quadrigemina; *f*, hemispheres.

Fig. LII.

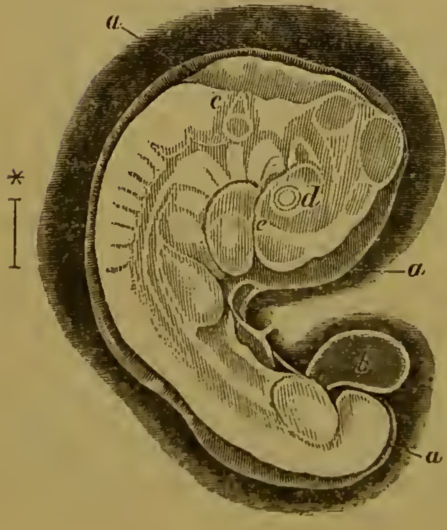

Fig. LII.—Embryo of the jackdaw (*corvus corone*) nearly four lines in length, drawn under the simple lens, the amnion, *a*, *a*, surrounds it closely on every side; the allantois, *b*, protrudes from the abdominal sulcus; the extremities are visible as simple lamellæ; numerous segments of the vertebræ and the several cerebral cells are conspicuous (vide figs. XLI. XLII. &c.); behind the corpora quadrigemina appears the cerebellum, and then the depression for the fourth ventricle; the ear is seen as a pediculated vesicle, *c*, springing from the medulla oblongata; under it lie the branchial arches and fissures; *d* is the eye; *e*, the nasal fossa, behind which the heart is perceived.

day, acquires nearly twice its former size, and inclines so much to the right side, that with the amnion, it covers the embyro completely, and comes in contact superiorly by means of its most vascular side with the serous envelope, which is consequently now completely separated from the amnion, to the formation of which it had in the first instance contributed. After the rupture of the vitellary membrane, all that remains of the albumen collects at the sharp end of the egg, and is now much more consistent; the yolk, on the contrary, has become much thinner and more diffluent, and the number of its globules has very greatly diminished; the embryo lies more towards the blunt pole of the egg, and on the sixth day, after breaking open the shell, the first

Fig. LIII.

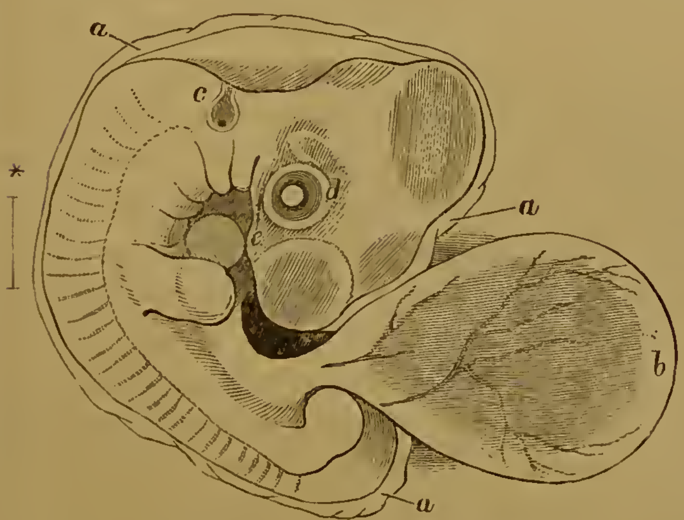

Fig. LIII.—An embryo similar to the last, but somewhat further advanced. The references are the same as in fig. LII.

Fig. LIV.

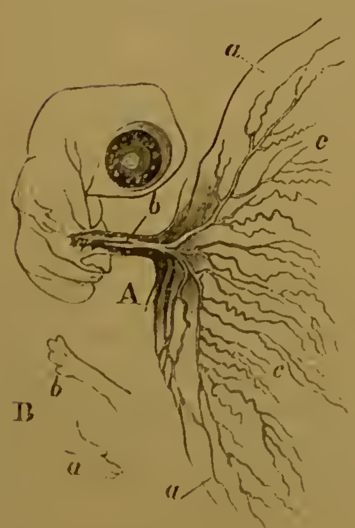

Fig. LIV.—Chick with part of the yolk *a*, *a*, which communicates by means of the delicate vitello-intestinal duct, with the noose of the jejunum *b*, which at this time lies within the funis umbilicalis; *c*, *c*, vasa lutea. *B*, separate views of the anterior extremity, which shows a distinct division into three digits, and of the posterior extremity, which shows traces of four digits.

appearances of motion arc observed in slight twitchings of the extremities [129].

§ 61. The most rcmarkable metamorphoses of the individual organs on the sixth and seventh days are the following: the spinous processes are now formed on the vertebral arches; the rudiments of the ribs becomc more conspicuous; the immediate tegument of the brain and spinal cord is perceived to be composed of two layers; the largely developed corpora quadrigemina seem to advance with less rapidity of growth towards the end of the seventh day, and the hemispheres soon equal them in size (fig. LV. *c, c, d, d*); the fornix is evolved over the still open third ventricle; the corpora striata and thalami become conspicuous; the optic nerves, distinct from one another at first, now become connected in the chiasma; the infundibulum is still deep and wide; the pituitary body appears; the cerebellum is formed; but the fourth ventricle is still widely open, and passes over into a deep posterior furrow of the spinal cord. The eye is developed in every part, and is very largc; the external opcning of the ear is conspicuous, and in connexion with the auditory vesicle the semicircular canals and cochlea are formed; the nasal depression has lengthened downwards into a nasal passage, which runs between the superior maxillary bone and the frontal process, the opposite halves of which have now become united. In the extremities, the arm and thigh, both extremely short, can be distinguished; in the hand the rudiments of the three digits, and in the foot those of the four toes, can be made out (fig. LIV. *B*). The amnion is more and more distended, and at the umbilieus is brought more together, so that it

[129] The whole of this period is so well described by Baer, and his observations and my own agree so eompletely, that I have had little to do but to follow him in the preceding paragraph.

FIG. LV.

Fig. LV.—An embryo somewhat older than that represented in fig. LI. surrounded by the amnion as an ample vesicle: *a*, the amnion; the eyes, *b, b*, are very largc; *c, c*, the eorpora quadrigemina, now searcely larger than the hemispheres, *d, d*; the space between them is the third ventriele.

becomes drawn out into an umbilical cord, in which lie the peduncle of the allantois and a noose of the intestine (fig. LIV. *A*, *b*); the neck advances in its evolution, and the lower jaw bones are elongated and assume the fashion of a beak. The heart acquires the form it possesses in after-life, the several parts having approximated and become more closely conjoined: the auricles are divided, and cover the ventricles, which can now even from without be perceived to be double; the aortal bulb at the same time appears produced from both ventricles in an arched form, arising directly over the septum, and being divided into two canals, the separation between which becomes visible outwardly on the seventh day; the pericardium is formed. From the aorta there now arise but two vascular arches on either side, and to the right a middle third arch; this and the two anterior arches are the later chief divisions of the aorta, and are filled by the stream of blood transmitted from the left ventricle; the two posterior arches are supplied on the seventh day with blood exclusively from the right ventricle of the heart, and are the future pulmonary arteries; the arches all terminate in the descending aorta. The Wolffian bodies, and the formations that take place upon or in connexion with them, have many remarkable relations during this period. The shut sacs of which they are composed become longer and more tortuous; they evidently secrete, and with their elongated common ducts, to which they look as if they were attached, terminate in the cloaca; betwixt their component shut sacs numbers of small points, which consist of little convoluted hanks of vessels, in every particular like the Malpighian bodies of the kidney, may be observed. The kidneys show themselves behind and above the Wolffian bodies on either side of the spinal column; at first they are lobulated greyish masses, which sprout by the outer edges of the Wolffian bodies; this is plainly to be seen on the sixth day, perhaps even sooner; the ureters are formed afterwards as their especial excretory ducts. The kidneys arise as independent formations; and, independently of them, the capsulæ suprarenales are evolved on their upper or anterior edge. The reproductive organs, which had appeared as little marginal lappets, now form two longish-shaped white bodies, and lie behind the suprarenal capsules, at some little distance from these, on the inner edge of the Wolffian body; they are still of like size, and it is impossible to distinguish whether testicles or ovaria will be produced; so that of all the principal organs the genital are those that are the latest recognizable in their rudiments, and distinguishable in their future special forms. The vessels of

the allantois are developed with great vigour; two arteries arise from the aorta, and a large vein runs on the under edge of the liver to the vena cava, along with the hepatic vein. The vessels of the allantois become the umbilical vessels.

The alterations that transpire in the mucous layer are of less moment: the organs already formed increase in size; the faucial cavity is elongated as the oral cavity in the bill-shaped maxillæ; the œsophagus extends; the division into crop and muscular stomach is distinguishable; behind the loop for the duodenum, and which encloses the pancreas, the jejunum forms a noose of the same length and tenuity, which lies completely out of the abdomen within the umbilical cord, where, by means of a delicate short conduit, it communicates with the vitelliele or yolk-sac,—the *ductus vitello-intestinalis* (fig. LIV. *A, a*). The liver is large and gorged with blood; the trachea and lungs are entirely separated from the œsophagus; the larynx makes its appearance as a small enlargement upon the trachea [130].

§ 62. The principal changes from the ninth to the eleventh day are as follow: the hemispheres of the brain enlarge greatly, at the cost, apparently, of the corpora quadrigemina, and span the third ventricle posteriorly; the cerebellum increases, particularly in its middle or vermiform portion, by which the fourth ventricle is now completely hidden; in the spinal cord the enlargements corresponding to the two pairs of extremities, become more conspicuous; the fibrous structure of the brain and spinal cord is apparent; the eyes proceed in their development, and attain still more colossal relative dimensions; the eye-lids appear as a circular-shaped fold of the skin; the external organ of hearing increases in width and depth. The bulbs of the feathers become apparent in certain districts, first along the middle line of the back, upon the haunches, and over the rump; the joints of the extremities are more solidly and distinctly evolved; the muscular parts are very apparent, and separated into bundles under the skin; the nerves are more conspicuous, and the motions of the embryo are stronger; the neck lengthens greatly. In the heart the external separation of the bulbus aortæ into two distinct canals follows; the vessel proceeding from the left ventricle gives off larger carotids from its anterior arch; on these appear the little thyroid bodies. These two aortal

130 The observations of Müller on the formation of the genital organs and corpora Wolffiana, agree with my own in every respect. On the same subject see Baer, l. c.

arches (*trunci anonymi*) represent the earlier third branchial vascular arch; the asymmetrical vascular arch that appears behind them, on the right side, is the future aorta descendens. From the stem arising out of the right ventricle proceed the two most posterior (the earlier fifth) of the branchial vascular arches; they do not yet give off any pulmonary branches, and still terminate posteriorly in the aorta; at a later period they become the proper pulmonary arteries. The corpora Wolffiana become shorter, and smaller every way, and their excretory duct longer; the kidneys increase in size. The germ-preparing sexual organs begin about this time to differ manifestly in their form: the testicles become elongated, cylindrical, and continue of equal size; the ovaries remain flattened, grow unequally, the right first ceasing to make any progress and then disappearing, the left enlarging proportionally with the other parts. The oviducts are distinct, but the right, like the ovary to which it corresponds, is arrested in its development. The gall-bladder becomes conspicuous as a diverticulum of the biliary duct. The *bursa Fabricii* emerges from the cloaca; the allantois grows still more over the embryo. The vessels on the vitellary membrane, especially on its under surface, are numerous and large; the veins are turgid and tortuous (fig. LIV. *A*, *c*), and appear stained of a yellow colour, whence they are often called *vasa lutea.*

§ 63. It is in the course of the last days of the second week that the epidermic formations are produced,—the feather bulbs, the nails, and the scaly coverings of the feet; ossification also begins in many bones, the muscular parts get stronger, the eyelids are well formed, and in the ear the tympanum has appeared. The Wolffian bodies are ever shorter and smaller; the testes acquire their excretory ducts; the left ovary is conspicuous, and the corresponding oviduct is hollow, whilst the same parts on the right side have shrunk entirely. The intestine makes several turns outside of the umbilicus, and continues in communication with the vitellary sac by means of the vitellary duct; upon the inner surface of the vitellary sac, and over the tortuous veins, membranous productions—puckered or wrinkled folds—make their appearance; and at the same time similar formations occur upon the mucous membrane of the intestine. The allantois has now grown completely around the embryo, so that the ovum—the vitellary sac, the remaining albumen, &c. included—is completely enveloped anew as it were, and will now retain its form even after the shell

is removed (fig. LVI. *b*; from the Kestril,—*Falco tinnunculus*); the serous covering disappears.

§ 64. In the beginning of the third week, the embryo, straitened for room, from the transverse axis of the egg comes more and more into the long axis, which it finally fills; the head is turned towards the breast, and mostly lies under the right wing; the allantois has inclosed the whole embryo and vitellary sac, and having contracted adhesions with itself forms an uninterrupted cyst or envelope for the entire contents of the egg, being everywhere in immediate contact with the membrane of the shell, from which it must be peeled when they are separated; in the interior of the allantois, white flocculent precipitates from the urine occur, and these accumulate at length to such an extent that they conceal the embryo in a greater or less degree. The allantois, as the

Fig. LVI.

Fig. LVI.—Embryo of the *Falco tinnunculus*, much farther advanced than that of the fig. LV. It is represented inclosed in its membranes, and of the natural size, but being removed from the shell, its weight has caused it to spread, and to look longer than it is in fact. The embryo of this falcon, by reason of the transparency of the membranes, is peculiarly fitted to serve for the demonstration of the relative position of the several parts: *a*, the embryo shining through the membranes; *f,f*, the eyes, of great size, seen from above; *b, b*, the allantois, has grown completely around the embryo, and so forms a perfect envelope, the chorion, whose principal vascular branches are perceived; *c, c*, the amnion; *d, d*, the yolk-sac; *e*, the albumen; *g*, the coccyx, with the feathers beginning to sprout.

Fig. LVII.

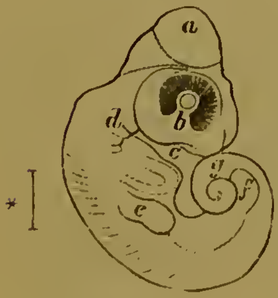

Fig. LVII.—Magnified view of the embryo of the *Lacerta agilis*, two and a half lines in length, for contrast with the other embryos figured: *a*, corpora quadrigemina; *b*, cleft of the eye; *c*, olfactory depression; *d*, branchial fissures already disappearing; *e*, anterior extremity; *f*, hinder extremity; *g*, tail.

complete fœtal envelope, is entitled the chorion. In the brain, the corpora quadrigemina, which have remained very much behind in development, are thrown backwards under the hemispheres; the pineal gland and cerebellum increase; the latter becomes marked with deep scissures. Over the eye, the eyelids grow till they meet, but without uniting; the iris advances, the cornea rises, the lenticular prominence remains, whilst the lens recedes, and so the anterior chamber, which had hitherto been wanting, is produced; there is no appearance of pupillary membrane. In the ear, the labyrinth becomes osseous at the beginning of the third week. In the heart, the valvular system is evolved; the anterior arteries are detached more and more from the descending aorta, and disappear altogether towards the end of the period; the pulmonary arteries become much larger, and their terminations in the aorta have contracted and become mere anastomosing channels—*ductus arteriosi.* The kidneys grow rapidly. The corpora Wolffiana shrink continually, but in male embryos they may still be detected as rudiments near the testes, even after the epoch of fœtal life is over. The right ovary, as has been stated, is arrested in its growth, and is soon after birth completely absorbed; the right oviduct also disappears, although a trace of it may be discovered in some birds at every period of their life. From the testes delicate vasa efferentia are developed, which, after passing through the Wolffian bodies, unite into a filiform vas deferens, which in its turn is evolved out of, or, more correctly, in the excretory duct of the Wolffian body. The vitellary sae shrinks more and more, its contents diminishing in quantity and becoming still more consistent. It is drawn into deep sacculated compartments by the main trunks of the umbilical vessels; the albumen and amniotic fluid are lessening continually in quantity. The tegumentary umbilicus is still freely open at the beginning of the last week; and with the advancing growth of the intestinal canal, a greater number of convolutions of the bowel pass out of the abdominal cavity; on the nineteenth day the prolapsed intestine returns in some degree into the abdomen again, and draws the yolk, with which it is still in uninterrupted connexion by means of the very considerable vitellary duct, along with it into the belly, upon which the mucous and vascular layers of the vitellary sac follow, whilst the serous layer increases, becomes thicker, and detaches itself from both the other layers. The whole vitellary sac is not thus taken up into the abdomen, only a part of it enters, and this expands in the cavity, whilst the part that is excluded is cut off by the contracting umbilical ring.

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The vitellary duct is of considerable width and arises funnel-shaped from the intestine; long after birth there is still a little diverticulum of the jejunum to be discovered in its former situation; nay, in some birds this diverticulum continues through life as a normal feature in their structure. The communication with the vitellus is at length obliterated, becoming a mere thread, on which a yellow knot, the last remains of the yolk, may not unfrequently be observed [131].

[131] There are two remarkable points in the above paragraph, which well deserve more particular consideration, from the light they are calculated to throw on the history of malformations from arrest of development: these are the deficiency in the right ovary and oviduct, and the persistence of the vitellary diverticulum in certain cases. I instituted researches upon these points in a considerable number of birds in my *Contributions to the Anatomy of Birds,* contained in the *Abhandlungen der Academie zu München,* II. 273 (1837). Later inquiries have only confirmed and extended the facts and views there announced. Notice of a few of the facts will suffice in this place. In all birds the rudiments of two ovaries and oviducts, symmetrical and of a size, are evolved; the degeneration and absorption of those on the right side occur among the several orders at different times, earliest among the passeres, the grallæ and palmipedes, and always during the fœtal period; later, and some time, longer or shorter, after birth, among the rapaces; here, indeed, it happens not unfrequently that the right ovary, in point of structure duly developed, and even containing true primary ova, which, however, do not seem susceptible of fecundation, exists through life; I have detected such a rudimentary formation at every period of life in many of the Falconidæ—in the buzzards particularly, and in the *falco gypäetus,* likewise in many owls, and among the parrots; Nitsch also discovered it in the eagles (I failed to find it in *pandion,* at least). In the *Falco palumbarius, F. nisus, F. æruginosus,* &c. the right ovary is regularly developed, and produces vitelli as proper for fecundation, apparently, as those of the left; of the right oviduct, however, either no trace, or a mere rudiment only, can be found. In those falcons even in which at a later period neither ovary nor oviduct occurs on the right side, their rudiments may still be found long after the fœtal period is at an end; in the half-fledged and fully-fledged nestling, they will usually be observed of about half the size of the corresponding parts on the left side. About this time the ovula become visible in the left ovary as dark masses, but not in the right, where the formative power is extinct, and no histological change occurs. The relations between the jejunal diverticulum, as the remains and representative of the ductus vitello-intestinalis, have a similar though opposite character. This part usually disappears in the rapacious, climbing, and singing birds, within a few days after birth, and seldom continues longer recognizable; it remains somewhat longer in many of the gallinaceæ, grallæ, and palmipedes; in the herons it is sometimes present, sometimes absent, and varies greatly in length, capacity, and form, in different individuals,—it occurs of one line and three lines in length. In many marsh and water-birds, as in the coot family, in the goose, but particularly in the Numeniadæ, this part continues to grow even after birth, attains to half an inch or an inch in length, communicates freely with the intestine, and continues through life as a normal delicate cœcal appendage; it

§ 65. *Birth of the Chick.*

Two days before its exclusion, the chick may occasionally be heard chirping feebly within the shell, for the chorion (the allantois) is readily torn by the point of the beak, which then comes into contact with the air contained in the air-chamber; along with the imperfect respiration that now goes on, the circulation through the umbilical vessels proceeds unimpeded. The violent motions of the chick occasion cracks in the shell; the beak assists, and holes are produced. The bill, so soft in all other parts, is furnished at this period with a very remarkable, hard, horny process near its point, evidently to enable the young creature to break through the shell, for the process in question falls off very shortly after the escape of the bird. The labour of getting free from the shell generally lasts half-a-day; at length the upper part is raised, the chick pushes out its feet, draws its head from under its wing, and erecting itself quits the shell completely. The remainders of the chorion and amnion, which, with the closure of the umbilicus, could no longer be nourished, shrivel, fall off, and are left behind in the shell [132].

§ 66. *Physical and Chemical changes in the Egg during Incubation.*

Various physical and chemical changes take place in the egg during the period of incubation. It loses weight: in the first week, to the extent of five per cent.; in the second, the amount is thirteen per cent.; and in the third, sixteen per cent. So that an

even presents determinate generic characters in regard to form and size, precisely as the cœcal appendages of the colon; in all the Fulicariæ, or coots, for example, it is very long, but delicate and narrow; it is more funnel-shaped in Numenius. With regard to the metamorphosis of the excretory canal of the Wolffian body into the vas deferens, the question may be found discussed in Müller (l. c. p. 32), who maintains, in opposition to Rathke, that the vas deferens is no new production, but a simple transformation of the excretory canal of the Wolffian body. To me, however, it appears that the vas deferens does arise as a solid thread in or upon the excretory duct of the body in question, a view in which Rathke seems now to participate. Vide in Burdach's *Physiologie*, ii. The decision of this point is of importance, as bearing upon the entire subject of development; and in reference to the question, as to how far new formations are to be regarded as transformations of pre-existing organs, or as arising severally and independently. On this point, vide the *General Physiology*, book iv.

[132] Baer has given a very detailed account of all that transpires shortly before the exclusion.—*History of Development*, i. 137.

incubated egg, with an embryo ready to emerge from it, is altogether lighter than one that is just laid; a new-laid egg sinks in water. —an egg at the end of the period of incubation swims. The cause of this loss of weight lies in the evaporation of the watery part of the albumen; the same thing happens, though more slowly, in unincubated eggs from keeping; the greater rapidity of the loss in the incubated egg arises merely from the greater heat to which it is subjected. Another eonsequenee of the evaporation is the formation and rapid enlargement of the air-space, whieh, as we have seen (§ 47), is first produced after the egg is laid. It is probable that the evaporation in question is connected with chemical changes, for the air contained in the blunt end of the egg is not simple atmospherieal air, but eontains a larger proportion of oxygen, the amount varying between 25 and 27 per cent. This hyper-oxygenated air serves the embryo in the process of respiration, or aeration, that is carried on by the medium of the allantois; for eggs may be incubated to the perfect maturity of the embryo, even without the eontact of the external atmospherie air, and may be hatched alike well in pure oxygen and in various irrespirable gases; for example, pure hydrogen, nitrogen, &c. At the beginning of the incubation the fluid albumen eontains a small quantity of oil, apparently communicated to it from the yolk; when the ineubation has advanced considerably, the albumen loses almost the whole of its water and salts (§ 21); these seem to be transferred to the yolk, which admits of explanation, for the vitellary sac bursts and draws the albumen, now changed into a thick mass, into it. By this aecession of matter, the yolk enlarges during the first half of the period of incubation, but becomes thinner; the incessant demand upon it, however, for materials for the growth of the embryo, eauses it again to shrink and to become more eonsistent towards the end of the period (§ 64). The proportion of ehemical elements of the vitellus and white vary considerably; the quantity of phosphorus eontained in the albumen lessens, but inereases in the yolk, and again appears in eombination with oxygen and calcium as a phosphate of lime, which in the period of the ossification is plentifully required for the consolidation of the bones; as the quantity of lime eontained in an egg at the time it is laid is extremely small (§ 21), and beeomes very large at a subsequent period, the earth must be acquired in some way with which we are not at present well acquainted. As it is not very probable that the lime is derived from the shell, it may perhaps be produced from other matters under the influenee of the organie agencies;

the same may be said of the iron, the quantity of which increases greatly during incubation [133].

CHAPTER II.

History of the development of the Human Embryo, with supplementary matter from the history of the development of Mammalia.

MATERIALS.

§ 67. EVER since the restoration of the sciences, the most distinguished anatomists and physiologists of their times have devoted themselves to the study of the development of the human embryo. In the descriptions and representations which they have left us among their writings, of preparations obtained from the

[133] However scanty and fragmentary our knowledge of the very remarkable chemical changes undergone during incubation, and however much all that has been reported on the matter wants confirmation and extension, still what we do possess is of exceeding interest. It seems impossible to mention any subject in organic chemistry which, carefully pursued, promises more copious results than the study of the alterations of the egg during incubation. For the particulars given above we are indebted almost exclusively to Prout.—Vide *Philos. Trans.* 1822. Bischoff was the first who discovered the fact of a larger quantity of oxygen being contained in the air of the air-cell, and the accuracy of the observation has been confirmed by Dulk. The experiments of Ehrmann, first communicated in the *Isis*, 1818, p. 122, showed that fecundated eggs might be incubated under irrespirable gases. [For Dr. Paris's analysis of the air contained in the air-chamber, see annot. 114, p. 88. The statement in the text, that eggs can be incubated to perfection in pure oxygen and neutral irrespirable gases, is certainly an error. The experiments of Schwann (contained in his *Diss. De necessitate aeris atmospherici ad Evolutionem Pulli in Ovo*, 4to. Berol. 1834,) have set the question for ever at rest, and demonstrated *that they can not*. In eggs *effectually* excluded from the contact of atmospheric air, no part of the future embryo is ever formed; the trifling changes that actually take place in the state of the cicatricula and halones probably only occur in virtue of the oxygen of the air-chamber. The law which declares the contact of oxygen necessary to the life of all that is organized, is so universal, that the experiments of single individuals ought never to be held as of any weight against it. Ehrmann erred and came to wrong conclusions, from not taking precautions against the *penetration* of the gases he used by the air of the atmosphere. Varnishes of organic animal matters, such as *albumen*, *gelatin*, &c. have no effect in preventing this *endosmosis* of different airs; and it was from overlooking this fact that Mr. Towne (*Guy's Hosp. Repts.* vol. iv.) erred. Had he *greased* his eggs, his results would have been different; every dairy-maid knows that an egg which has been well greased to make it keep, will not produce a chick when set under a fowl, but will in due season become addled.—R. W. Mr. Towne's very recent experiments only show that eggs

bodies of women who had died or who had miscarried at different periods of their pregnaney, we have a great mass of materials, but they are merely fragmentary, and very dissimilar in point of worth. The rare occurrence of opportunities to examine the bodies of women who have died in the earlier periods of their pregnancy in a recent state; the uncertainty of all observations made on ova which have been cast off by abortion; the difficulty of drawing correct inferences in regard to the mode of origin of certain formations from their anatomical characters only; finally, the prejudices and preconceived opinions of writers, and the false views of things, correctly observed in themselves, to which these lead;—such are the chief obstacles that oppose themselves to a connected and clear apprehension of the first stages in the development of the human embryo. We are therefore, and almost of necessity, here compelled to have recourse to the mammalia as sources of information, and not only in regard to these earlier periods, but even as concerns much later stages in the history of development; and there can be no doubt that researches on the mammalia earefully conducted, and used with diseretion, are much better calculated to throw light on the primary formation of the human embryo than any amount of necessarily unconnected observations on human ova cast off at an early period, and in the great majority of cases obviously diseased. The history of the evolution of the human fœtus at later periods is so complete in itself, from the number of observations we now possess, that there is scarcely any necessity for recurring to the mammalia in regard to it. In treating the whole of this subject, the history of the development of the chick is still the safest guide, and to this we shall therefore continually refer[134].

whieh have been coated over with albumen and covered with several layers of paper dipped in that fluid, can be incubated to the complete evolution of the embryo; not that the embryo can be produeed without all access of atmospheric air.—R. B. T. With regard to the supposition that the lime which enters in such large quantity at last into the body of the chiek is produeed *"from other matters under the influence of the organic agencies,"* this is quite inadmissible in the present state of ehemical science. Neither indeed is there any occasion for such an impossibility. The shell of the fully incubated egg is always light, brittle, and spongy, and careful investigation would eertainly show that all the lime in the composition of the ehiek was derived from this source.—R. W.]

[134] The works that treat most fully of the matters now to engage us are the Physiology of Burdach, ii. and the Manual of Development of Valentin (*Handbuch der Entwickelungsgeschichte des Menschen*), Berl. 1835. The greater number of the newer elementary works on physiology, based on individual observation, have not yet reached the subjeet of development. Döllinger only in his Elements of Physiology, (*Grundzügen*, 1st part, 1835,) and Heusinger in his *Notes*

§ 68. *Earliest appearances of Conception in Mammalia; detachment of ova; production of corpora lutea.*

At the season of heat in mammalia, individual ova come to maturity in the Graafian vesicles; after the intercourse of the sexes an increased flow of blood takes place to the ovaria; the vascular membrane of the Graafian vesicle enlarges; the granules or

to a Translation of Majendie's Physiology, 2d vo ., 1836, treat this subject by the way, and briefly. Among the elementary anatomical works, that of Lauth, *Elémens d'Anatomie Pratique,* 2d vol. 1836, contains a short but very precise, clear, and comprehensive account of the evolution of the fœtus, illustrated by diagrams. In Weber's edition of *Hildebrandt's Anatomy,* there is an excellent account of the evolution of each individual organ or system, and of the anatomy of the fœtal membranes. Among iconographic works, that of Dr. Wm. Hunter, *The Anatomy of the Human Gravid Uterus,* fol. max. 1774, deserves particular mention as unsurpassed in accuracy of representation and beauty of execution. The best figures of the external forms of the embryo are still those of Soemmering, *Icones Embryonum,* 1799. Among later works, that of Velpeau, entitled *Embryologie ou Ovologie humaine,* Paris, 1835, must be mentioned. Many of the earlier ova there represented are certainly diseased. The *Etudes Anatomiques, &c. de l'Œuf* of Breschet, Paris, 1832, are distinguished by the excellence of the representations of healthy as well as of diseased ova. The work of Seiler, entitled, "The Uterus and Ovum of Man in the earlier months of Pregnancy," (*die Gebärmutter und das Ei des Menschen in den ersten Schwangerschaftsmonaten dargestellt,*) Dresden, 1832, contains several beautiful and faithful figures; unfortunately the work is not finished. The subject is treated systematically and iconographically in Flourens' *Cours sur la Génération, l'Ovologie, et l'Embryologie, publié par Deschamps,* Paris 1836; but imperfectly and without reference to the latest discoveries. The same may be said of the production of M. Coste: —*Embryogénie comparée; Cours sur le Développement de l'Homme et des Animaux,* tom. i. Paris, 1837,—a work which, with a little of high pretence, certainly contains much valuable matter, illustrated by good figures in connexion with the development of a few of the mammalia, viz. the sheep, the dog, and the rabbit; but in which the development of the human embryo is most imperfectly and unsatisfactorily treated. For the most important and also the latest contributions on the developement of the mammalia of all orders and also of man, we are beholden to Baer (*Entwickelungsgeschichte der Thiere,* 2 Bde, 4to, Königsb. 1828—37). These are contained in the second volume of his great work, which it is much to be regretted is yet unfinished, and unprovided with explanations of the plates. Kilian, in his *Geburtshülflicher Atlas,* 1837, has given an excellent selection of the best plates extant of the fœtus and uterus, to which he has added many of interest peculiar to himself. I have here mentioned only the very principal works that treat of development; in no part of anatomy and physiology perhaps are the materials so widely scattered through periodical publications, contained in small tracts, &c.: the chief contributors in this way are Bojanus, Meckel, E. H. Weber, Rathke, Burdach, J. Müller. [T. Wharton Jones, M. Barry, and C. Reichert.]

cells mingled with its contents, become greatly developed and altered [135]; and a thickening and general increase of its walls, particularly of the base and sides (fig. LVIII. *B*, *b*, from the bitch), ensue, precisely as in the capsule or calyx of the bird (fig. IX. *a*, p. 38); the ovum and other contents of the follicle are by this pressed forwards, or against that aspect of the follicle which is in contact with the peritoneum, and which now becomes continually thinner and thinner, and finally bursts, so that the ovum escapes (fig. LVIII. *B*, *d*; fig. XIV. *c*, p. 46), and a cavity is left in the ovary (fig. LVIII. *c*, LIX. LX. *a*, and XIV. *b*;) this is soon obli-

[135] In a bitch forty-eight hours after intercourse, I found the Graafian vesicles of three or four times their original dimensions, and surrounded by a vascular rete, as is described and figured with reference to birds. (fig. XXIV.) The granules of the contents had become large oval cells, completely filled with dark molecules, and the nucleus as clear as a transparent vesicle, so that these cells bore the strongest resemblance to the pigmentary cells of the choroid of the eye (fig. LXI.); some of the cells were smaller, paler, and without any darker molecular contents.

Fig. LVIII.

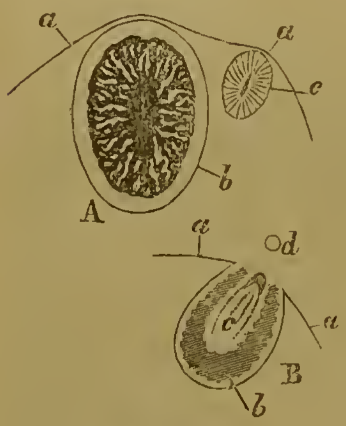

Fig. LVIII.—A section of a portion of the ovary of the sow; *a*, *a*, investing peritoneum; *b*, recent corpus luteum full of black blood; *c*, older corpus luteum; *B*, Graafian follicle of the bitch, just burst, magnified and partly as a plan, after Baer; *a*, *a*, investing peritoneum; *b*, fleshy mass formed around the walls of the follicle; *d*, the ovulum which has escaped.

Fig. LIX.

Fig. LIX.—A corpus luteum from the body of a female who destroyed herself by drowning, eight days after impregnation; *a*, mucous tunic of the Graafian vesicle sprouting from the circumference towards the centre; *b*, external tunic of the Graafian vesicle; *d*, investing membrane of the ovary; *c*, ovarian stroma; *e*, point at which the ovulum escaped from the Graafian follicle. (After Baer, in *Siebold's Journ. f. Geburtschulfe*, b. xiv. t. i.)

Fig. LX.

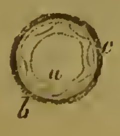

Fig. LX.—Section of a Graafian vesicle of a female, who also committed suicide by drowning, having been in the company of an admirer the day before. The inner membrane *a*, is thickened, and in folds; *b*, the outer membrane; *c*, ovarian stroma. (After von Baer, in *Siebold's Journal*, u. s.)

terated, by the growth on all sides of the inner membrane of the follicle—a reddish fleshy-looking mass sprouts from the walls towards the shrinking cavity, and the rent by which the ovum had escaped is finally closed[136]. An ovarian follicle thus altered

[136] In addition to the matters in the text, Baer goes on to say:—"The empty capsules in birds do, in fact, occasionally assume the appearance of the corpora lutea of the mammalia, especially when the edges of the cicatrice, as happens occasionally, again coalesce. But, even when the edges do not coalesce, the shrivelled and greatly diminished calyx, which also acquires a yellow colour, bears a striking resemblance to an unclosed, but very small corpus luteum of a mammiferous animal," *Entwickelungsgeschichte*, p. 182. Corpora lutea are always to be viewed as so many indications of previously fecundated and ruptured Graafian vesicles. Meckel, in his *Anatomy*, vol. iv. p. 686, says:—"I am strongly inclined to regard all the accounts we have of differences in the number of corpora lutea, and the young produced, as the effects of imperfect or erroneous observation; in more than two hundred instances in which I have examined the ovaria of women who had had families, and of the females of mammalia of different kinds which had been pregnant, I have, without any exception, found the number of corpora lutea to correspond with the number of children, or of the young that had been borne. The best observers—Haller, Hunter, came to the same conclusion."

[There are, however, other opinions on the cause and mode of formation of the corpus luteum, besides that given in the text and note above, which it seems right to mention here. Dr. Montgomery, of Dublin, for instance, holds, that it is no increase or production of the inner coat of the Graafian vesicle, but a new formation between the two layers of membrane composing that cyst (*Exposition of the Signs of Pregnancy*, p. 219. 8vo. Lond. 1837). Dr. R. Lee again concludes from his observations, that the body in question is formed around, or on the outside of both coats of the vesicle, the yellow matter deposited being in immediate contact with the stroma of the ovary (*Med. Chirurg. Trans.* vol. xxii. Lond. 1839). Dr. Paterson, the last writer on this subject (*Obs. on Corp. Lutea*, in *Edinb. Med. and Surg. Journal*, for January, 1840), espouses Dr. Montgomery's conclusions. "It is the vascular *covering of the ovisac*," says Dr. Barry, "which becomes the corpus luteum, not the inner membrane of the Graafian vesicle, for that inner membrane is constituted by the ovisac itself, which disappears."—*Researches*, 2d series, p. 318 and 350. The views of British inquirers are essentially the same; the difference between them merely refers to the parts which each assigns to the Graafian vesicle and to the ovary, connected with their skill severally in splitting these into layers. Whether the deposit take place around one or two coats of the Graafian vesicle is perhaps of little moment; it is certainly on the outside of so much of the Graafian vesicle, viz. the lining membrane of the cyst, as nature has no farther use for, the end of the deposit being doubtless to isolate from the rest of the organism that which has already fulfilled its office. And here the interesting question presents itself in regard to the significance of corpora lutea under any circumstances. We have seen recent general opinion to be, that ova are normally cast loose at each menstrual period in women, and each season of heat in animals (Annot. 88, to § 33). The breach in the ovary which is the consequence of this phenomenon must be repaired, and it would actually seem to be made

is known by the name of *corpus luteum;* in man, and many mammalia, the colour is yellow at length; in others, it is reddish or whitish. In many mammalia, the corpus luteum grows to a considerable size; in the sow, for instance, the corpora lutea continue for some time after the separation of the ova in the form of large livid or purplish red berries (fig. XII. *a, a,* p. 45), their cavities being filled with coagulated blood, which occasionally exhibits a peculiar dendritic appearance (fig. LVIII. A, *b.*) By the side of the more recent corpora lutea it is usual to find smaller shrunk bodies of the same kind, the results of former conceptions (fig. XII. *b, b*), which are really yellow, and about half the size of ripe unemptied follicles (*c, c, c*); when cut across, they show the mode in which they have been consolidated by the growth of the inner parietes, which have filled the cavity completely, nothing being left of it save a little cleft or cicatrix (fig. LVIII. *A, c*). The mechanism, by which the ova in the mammalia are cast loose from the ovary, would therefore appear to differ much less from that which obtains among birds than might at first sight be imagined. By the growth of the walls of the calyx or capsule, the yolk in birds is carried outwards, pressed against the peritoneum, and pushed from the stroma (§ 48); in mammalia, the process is in every particular the same; the identity of the process is even more striking, when animals, which have a

good in the same way, but somewhat modified, as the rupture in the ovary which is the effect of impregnation. Physiologists, at the present day, therefore, very uniformly recognise *true* corpora lutea, and *false* corpora lutea, the former being the effect of impregnation, the latter of the escape of an ovum that has not felt the influence of the male. *True* corpora lutea are, at first, much larger than false corpora lutea; they are also of a pretty regularly round figure; they present concentric radii when divided perpendicularly; their centre is occupied by a distinct membrane (the lining membrane of the Graafian vesicle,) they have a puckered central cicatrice, and they are never numerous. *False* corpora lutea again are small and irregular in form; they want the central cavity lined with a distinct membrane; they show no puckered central cicatrice, and no concentric radii on the surface of a perpendicular section; finally, they are frequently numerous and demonstrable in both ovaries. R. W.]

Fig. LXI.

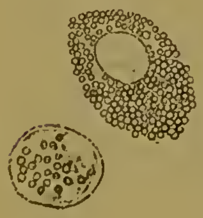

Fig. LXI.—Two cells from the granular membrane of the fœcundated Graafian vesicle of a bitch, forty-eight hours after conception. The larger cell surrounds a very bright nucleus, and is filled with dark molecules, so that it bears a strong resemblance to a pigmentary cell of the choroid coat of the eye.

scanty ovarian stroma, and in which the follicles are pediculated like berries, as in the mole, and still more in the ornithorhynchus (fig. XIII. *a*, p. 45,) are contrasted; the ovaria, in these creatures, are extremely like those of birds (fig. XXIV.); the difference between them lies almost solely in the presence of the additional particular granular mass in the Graafian follicle of the mammal*.

§ 69. *Progress of the Ovum in the Fallopian tube, to its arrival in the uterus.*

Of all the particular points in the history of development, the reception of the ovum by the Fallopian tube, and its progress to the uterus, are those that still lie hidden in the deepest obscurity. No one has yet succeeded in discovering ova in the Fallopian tube of the human subject; all the accounts of such a thing having actually been seen are more than doubtful: even in the mammalia, among which the precise moment of impregnation is known, it is one of the most delicate and difficult of anatomical researches to discover bodies so minute as the ova in the Fallopian tubes. It would appear, too, that the term at which the ova arrive in the uterus is not precisely the same even in the same species of animal; it may vary several days in every kind; in rabbits, for instance, the ova reach the uterus from the third to the fifth day after impregnation; in the bitch, the period is much longer, the ova not attaining the uterus till after the lapse of ten or twelve days. In the animals just named, the earliest periods in the development of which are the best known, several ova are detached, and arrive successively, rarely together, in the uterus; and it would seem that the Graafian vesicles do not, by any means, all give way at the same time, but that individual follicles burst several days earlier than others. During the whole of this period, the infundibulum of the tube or oviduct grasps the ovary, and adheres to it closely, so that the ova, as they escape from the vesicles, necessarily pass into its abdominal extremity. To what extent the muscular contractions of the Fallopian tubes, or the ciliary motions of their epithelial indusia contribute to the farther

[* The ovum is expelled from the Graafian vessel, owing to a *vis à tergo* produced by the thickening of the base and sides of the vesicle. This *vis* acts, of course, not upon the minute ovum only, but upon the contents of the vesicle at large, which are, therefore, in part at least, expelled along with the ovum. R. W.]

progress of the ova is unknown. Occasionally the ovaria remain for weeks closely grasped by the infundibula of the tube.

With regard to the ova themselves, they [were believed, till very recently, to] undergo but little alteration during their passage through the tubes; they carry off a small portion of the granular stratum of the vesicle with them, which appears hanging to them at first as an irregular, ragged discoidal appendage (fig. LXII. and LXIII.), but this is soon detached; with this the chorion enlarges; the stratum that surrounds the vitellus becomes more consistent, and does not escape along with the thinner contents when the ovum is punctured; the ovum gains a little in size, too, during its progress through the tube, perhaps by absorbing the fluid resembling thin albumen, which is shed into the tube at this time; the yolk becomes more readily separable from the chorion; there is still no trace of any especial spot where the embryo arises[137].

[137] Dr. Bischoff, of Heidelberg, has kindly transmitted to the author an account of a complete series of observations upon ova, in their progress through the Fallopian tubes, in the bitch, of which an abstract follows. Dr. Bischoff says:—" With regard to the period at which the ovum escapes from the ovary, I believe I may safely aver, that it is very various, and often both much earlier and much later than is generally believed. The earliest period at which I have observed it to occur is thirty-six hours after intercourse; this was in a pointer bitch (Spitzhundin), which belonged to the servant of our anatomical

Fig. LXII.

Fig. LXII.—A fully ripe ovum from the ovary of a rabbit in heat, surrounded by the proligerous disc, magnified 290 diameters. The cells of the disc are crowded with molecules, but their boundaries are not discernible, from the ovum being drawn, still included within the Graafian follicle; in the vicinity of the germinal vesicle, the vitellary fluid is perceived almost wholly free from granules, vide fig.

[The enquiries of British embryologists have shown the ovum to be the seat of very great and important changes, both before it is

theatre, and who had taken a note of the precise time of the coitus. The ova were, in this instance, already in the middle of the tubes. In another bitch, which I examined nineteen hours after intercourse for the first time, the ova had not yet escaped from the Graafian vesicles, six of which, however, were very much enlarged, but still completely closed; I detected the ovum in each of these. In another young bitch, which had not suffered any dog to approach her for fourteen days, although she was still in heat, and a bloody fluid escaped from the vagina, I found the ova, to my great astonishment, still in the middle of the tubes, as in the case examined after a lapse of only thirty-six hours. In another bitch, which had not submitted to the male for eleven days, the ova were still very backward, having just passed from the tubes into the uterus. These three last mentioned cases were all first conceptions; the animals were all young, and had not previously had litters. In older bitches, on the other hand, I generally found the ova farther on than I had expected. I am inclined to believe that age is the principal cause of the differences observed in this respect: in young bitches, impregnated for the first time, the ova are both detached from the ovaries later, and move through the tubes more slowly than in older animals, which have already littered once or oftener. Besides this, the degree of the heat, as already remarked by Von Baer and by Guenther, appears to have some influence. To discover the ova in the tubes, I begin, by removing these from the ovaria and all connected parts, so that all tortuosity disappears, and nothing remains adherent to them. I then stretch them out with a pin or pins at each end upon a red or black waxen tablet, and slit them open from the abdominal

Fig. LXIII.

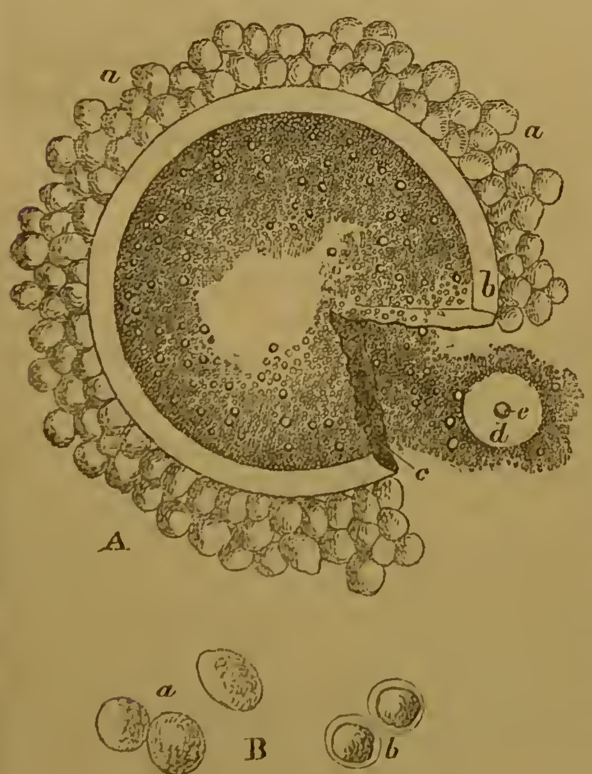

Fig. LXIII. *A*, *B*.—An ovum of a rabbit not quite ripe, magnified 290 diameters, removed from the Graafian vesicle, and burst under the compressor,—*a*, *a*, granules or cells of the proligerous disc; *b*, the thick chorion [?] (zona pellucida); *c*, rent in this membrane, through which the contents of the vitellus, and the germinal vesicle *d*, has escaped; the nucleus of the germinal vesicle is apparent as usual as the germinal spot *e*; *B*, highly magnified granules from the contents of the Graafian vesicle; *a*, the granules without preparation; *b*, the granules treated with dilute acetic acid, and the involucre of the cell thereby separated slightly from the nucleus.

cast loose from the ovary, and during its passage through the Fallopian tube. In the ovary it acquires an outer membrane, which

end onwards with a pair of fine sharp scissors. I now search every fold of the divided tube with care, and have almost always been so fortunate as to discover all the ova in the tube, generally at no great distance from one another. It is only necessary to be well acquainted with the appearance of the ovarian ova, and to have a quick eye, in order to succeed. The ova of the bitch, by reason of the denseness of their vitelli, are perhaps more easy to find than those of any other animal, which causes them to look like white points. I then remove the ova carefully with a needle to a glass tablet, and examine them as quickly as possible under the microscope, without addition of any kind, as I find that fluids of every description cause changes in the ova, particularly in the form of the yolk; saliva causes, perhaps, as little change as anything, and this I use when moisture becomes indispensable. The highest point at which I have found ova has been about the upper third of the tube, which was in a bitch thirty-six hours after her first intercourse, and in another, which was killed during the continuance of the heat, but without my having had an opportunity of knowing the exact time of the intercourse. All the ova I have found in the tubes have borne a strong resemblance to those of the ovaria; they all presented a granular disc, exactly like that which they exhibit in the ovary, and the vitellus was always opaque and dark. The earlier of them also showed almost no alteration in point of size, and in the appearance of the vitellus. But I searched with the greatest perseverance, and with every possible precaution, for the germinal vesicle, in vain. I believe, therefore, that I am in a condition to announce the disappearance of this structure in the ova of the mammalia as an ascertained fact, whereas it has hitherto only been presumed hypothetically, or from analogy. In the pregnant bitch which I examined nineteen hours after the first intercourse, and in which I found the ova still in the ovaria, these still contained their germinal vesicles. The germinal vesicle, therefore, in all probability, only disappears on the escape of the ovum from the ovary. What becomes of it I cannot positively say; I feel persuaded, however, that it bursts, and that its contents, mixed with the sperma of the male, form the macula, from which the development of the embryo proceeds. The farther changes which the ovum undergoes in its progress through the oviduct, are the following:—1. It increases in size, but not very remarkably. 2. The yolk obviously acquires greater consistency, its granules cohere more strongly. When an ovarian ovum is ruptured with a needle, the vitelline granules immediately escape, and diffuse themselves in the water; but I have divided impregnated ova of the tube with the needle into two, four, or six pieces, without the vitellus becoming diffused; the portion of yolk connected with each little segment remained adherent to it, and seemed quite coherent; when forcibly mixed with water, still the granules did not separate completely; they always remained in groups or clusters.—3. Changes in the form of the vitellus takes place. Whilst this part in ovarian ova lies close to the inner surface of the vitelline membrane,—I mean the chorion or zona pellucida,—this was only the case in the earliest ova from the tubes; in all the others it seems to quit this surface in different points, and, instead of its original round form, it now looks angular and uneven. I have occasionally observed such remarkable forms, that I asked myself the question, whether the vitellus of the mammiferous animal's ovum underwent changes of form similar to those of the ovum of fishes and batrachia?

in the tube becomes swoln with moisture, and assumes the appearance of a thick gelatinous-looking membrane—the PROPER CHO-

Unfortunately these forms of the ova are very rapidly lost, when the ova are moistened with water or saliva, apparently from imbibition of the fluid. I have not found it possible, on this account, to make drawings of several of the forms I have observed.—4. In many of those ova from near the uterine end of the duct, I have imagined that I could distinguish a very delicate membrane surrounding the vitellus internally. I could never succeed, however, in isolating this membrane, or seeing it by itself, so that I dare not speak on this point more decidedly.—5. On the other hand, it is quite certain, that the ovum receives no new external covering in the course of the duct or tube; it acquires no albuminous layer or membrane like that which lines the shell in birds; and I can therefore state positively, that the outer covering of the ovarian ovum also remains the outer covering (always putting the decidua out of the question) of the tubular and uterine ovum through all its stages,—a fact, which Von Baer, Wagner, Coste, and others, had merely spoken of as probable. Mr. T. Wharton Jones, the only observer who believes that he has seen this formation of albumen and membrane, was probably deceived by the disc. He has either not been sufficiently well-acquainted with this part from the ovary onwards, or no longer expected it in the impregnated ovum (as it actually does disappear at a later period), and has taken its granules for the albumen forming around it." Little can be added to these laborious and careful researches of Bischoff. Whether there be any mistake or not about the alteration in the form of the vitellus must be determined by future inquiry. I have not yet, myself, succeeded in discovering ova in the tubes, in the few attempts I have made in this direction. Among the older inquirers, De Graaf (op. cit.) followed the first stages in the conception of the rabbit with diligence; and, had he but been acquainted with the true ovum, and examined it microscopically, we should long have been in possession of the wished-for information. Three days after intercourse, De Graaf found the ovary closely embraced by the infundibulum of the tube, and one ovum in the tube, and two in the uterus of the right side. Cruikshank, who repeated De Graaf's experiments with great care, on many occasions found ova in the infundibula, on the third and fourth days after intercourse; they appeared to have increased somewhat in size. Prevost and Dumas found the ova in the tubes in bitches eight days after intercourse (*Ann. des Sc. Nat.* vol. iii. p. 122) Baer found the ovule in the tubes of a bitch; it was only slightly enlarged, and appeared somewhat loosened in its texture, in comparison with its form and appearances in the ovary; he also observed the ovum of a sheep in the same state, even before the end of the first day; the proligerous disc (the granular disc) was much loosened and diminished. *Entwickelungsgeschichte,* ii. p. 183. The period during which the infundibulum grasps the ovary, also appears subject to great variations; a fact, which was remarked by most of the old observers. Baer says, that in the sow, the ovary generally continues embraced for about four weeks; in the sheep, the period is nearly the same. This, however, is not invariably the rule; I have found it free in the sow eight and ten days after intercourse.

[The observations of Mr. T. Wharton Jones, alluded to by Dr. Bischoff, were to the effect, that, having found ova in the Fallopian tubes, near where they enter the horns of the uterus in a rabbit, the third day after impregnation, he saw these ova remarkably different in their appearance from the ova as they exist in

rion. By and by the zona pellucida, which is visible at first, having disappeared, the newly-formed chorion comes to be the

the ovaries themselves. In addition to the component parts of the ovarian ovum, he perceived that they had a thick transparent investment similar to that which is observed in the ovum of the frog. Subsequent observations led Mr. Jones to conclude, that this additional transparent investment was acquired in the ovary, that it was different from the zona pellucida, which he regards as the proper vitellary membrane, and that this new investment, and not the zona pellucida, formed the proper chorion. In one observation, made on the rabbit seven days after impregnation, he found the new transparent investment indicated, to constitute the sole covering of the yolk, but it formed a large cavity when compared with this part in point of size. Here he supposed the zona pellucida to have disappeared, in the same way as he directly observed it to do in the ova of the newt. In a human ovum, aborted at a very early period, the same careful observer farther found that the thick transparent membrane (zona pellucida), had disappeared, or been resolved into a gelatinous cellular tissue, which filled the new investment,—the chorion. Imbedded in this peculiar tissue, a small round body was discovered, which proved to be the yolk now forming a spherical blastoderma. *Philos. Trans.* 1837, p. 339.

In § 20, and the annotations to it, particularly annot. 56, justice was not done to the highly meritorious observer whose name has but just been mentioned—T. Wharton Jones: let it be rendered here. Wharton Jones was, beyond all doubt, the discoverer independently, but contemporaneously with others, of the germinal vesicle and germinal spot in the ovum of man and mammiferous animals. His observations were made in September 1834, and his discoveries were shown to many at the time and immediately afterwards: the present distinguished professor of General Anatomy and Physiology in University College, London, Dr. Sharpey, has informed the writer of this note, that he had seen Mr. Jones, in his demonstrations of the ovum in the sheep, turn out the germinal vesicle from its cavity, and indicate the germinal spot upon it, in the beginning of the month of February, 1835. Mr. Jones, in the course of the same month, embodied his observations in a paper which was sent to the Royal Society, accompanied with drawings of the various structures he had seen. The originals—the paper and drawings now in the archives of the Royal Society, have been inspected by the writer of this note, and there can be no doubt of the facts as stated. The views at this time current in Great Britain, with regard to the structure of the ovum, were those of Baer, and to the effect that the ovum of the mammiferous animal was the analogue of the Purkinjian vesicle of the bird's egg, the Graafian vesicle at large of the mammal being held as corresponding to the vitellus with its contents, in the bird. Mr. Jones had the honour, as an independent inquirer, of entering the field on this particular against Von Baer, and of fairly confuting him. Mr. Jones is therefore the original interpreter among us of the important discovery of Baer, and he is as much the discoverer of the germinal vesicle as Coste, or Bernhardt and Valentin, and of the germinal spot, as the author of this work. By some strange error Mr. Jones's paper was not printed in the transactions of the Royal Society, which it would have eminently graced. It only made its appearance subsequently in the pages of the *London Medical Gazette*, and it is by the kind permission of the editor and proprietors of this excellent

sole investment of the yolk. Several large and transparent vesicles arise in the centre of the yolk (fig. LXIV. *B, C*); by and by

periodical, that Mr. Jones's figures and explanations are here added. Mr. Wharton Jones has also the undoubted honour of having discovered the true chorion as a formation posterior to the act of impregnation. His view of the *zona pellucida* of the mammiferous ovum as the analogue of the *membrana vitelli* of that of the bird, is now also beginning to be admitted by all physiologists. There is no British physiologist to whom the science of Embryology stands nearly so much indebted as to Mr. Jones: he is not only the most original, but probably the most successful of all our inquirers into this difficult subject. R. W.]

Figures which illustrate Mr. T. Wharton Jones's paper, entitled, 'On the Ova of Man and Mammiferous Animals, as they exist in the ovaries before impregnation; and on the discovery in them of a vesicle analogous to that described by Prof. Purkinje, *in the immature egg of the Bird.' Read at the Royal Society,* 1835.

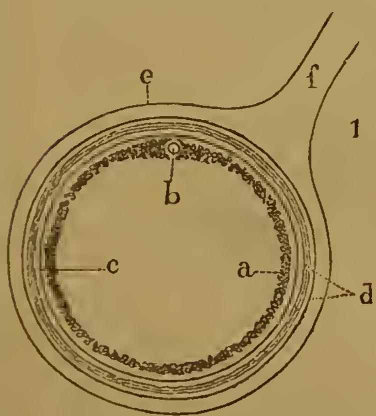

Fig. 1.—Diagram representing a section of the hen's egg within the capsule of the ovary, and the position of the vesicle of Purkinje.—*a*, The granulary membrane, forming the periphery of the yolk; *b*, the vesicle of Purkinje embedded in the cumulus; *c*, the vitellary membrane; *d*, the inner and outer layers of the capsule of the ovum; *e*, the indusium of the ovary; betwixt the indusium and the capsule the stroma is seated; *f*, the pedicle by which the capsule is attached to the ovary.

Fig. LXIV.

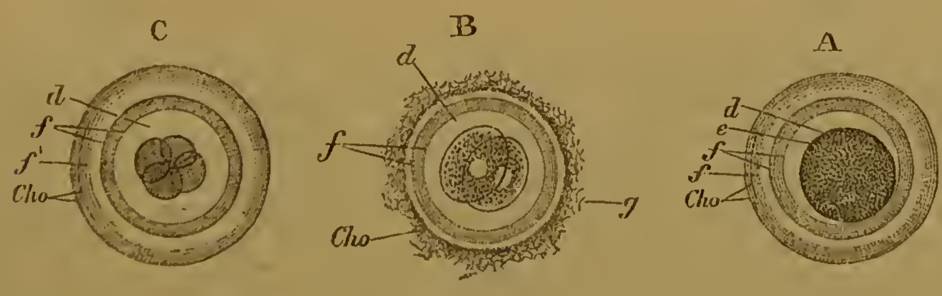

Fig. LXIV.—Ova of the rabbit from the Fallopian tube (after Barry). *A*, ovum of 35¾ hours, $\frac{1}{10}$th in diameter, found near the middle of the Fallopian tube; *B*, ovum found at the middle of Fallopian tube, more advanced than *A*; *C*, ovum also from Fallopian tube, and still more advanced than *B*; *cho.* chorion *f*, zona pellucida; *e*, vitelline membrane; *d*, yolk; *f'*, fluid imbibed by the chorion.

these disappear, giving place to a smaller and more numerous set (figs. LXVIII. and LXX.) which, in their turn, yield to others

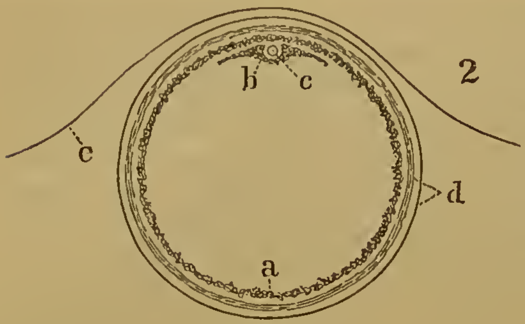

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Fig. 2.—Diagram of a section of the Graafian vesicle and its contents, showing the situation of the ovum.—*a*, The granulary membrane; *b*, the proligerous disc; *c*, ovum; *d*, the inner and outer layers of the wall of the Graafian vesicle; *e*, indusium of the ovary derived from the peritoneum, the stroma immediately underneath which is condensed so as to form the *tunica albuginea*.

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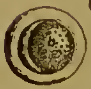

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Fig. 3.—The human ovum as seen under the microscope by transmitted light, magnified forty-five diameters *. On one part of its surface a small spot is seen, which is the elevation on the side of the germinal vesicle [the germinal spot]. Fig. 4.—The ovum still surrounded by the proligerous disc, magnified about fifteen diameters Fig. 5.—The outer envelope of the ovum lacerated, and the granulary membranous sac composing the yolk drawn out. Fig. 6.—A human ovum magnified forty-five diameters, in which the granulary sac is so much contracted that it does not fill up the whole cavity of the external envelope †. The spot on the

* The measurements given do not lay claim to any very great accuracy, as they were made with a micrometer glass under the simple microscope.

† The distention of the external envelope, by the absorption of water, and not the contraction of the granulary sac, may be the correct explanation of this appearance.

still smaller, and still more numerous (fig. LXV.) and the same thing happens repeatedly, until a coarsely granular structure is

surface of the granulary sac, which may be considered as the cicatricula, is the elevation on the side of the germinal vesicle. Fig. 7—represents, within a square area, the human germinal vesicle, magnified forty-five diameters. On one side of it is seen the small elevation, [the germinal spot]. Fig. 8.—A human ovum, magnified forty-five diameters. In it the grains composing the granulary sac were in such small quantity, and adhered so little together, that the whole germinal vesicle [with its spot], is seen shining through the outer envelope. Fig. 9 is a diagram of a section of an ovum, representing the thick external envelope, within which is the granulary sac, and, connected with the inner surface of the latter, the germinal vesicle. Fig. 10 represents a human ovum, which I found in the ovary of a married woman of about 30. It is somewhat like two joined together, but there is only one germinal vesicle.

Figures which illustrate Mr. T. Wharton Jones's paper, 'On the first changes in the Ova of the Mammifera in consequence of Impregnation, and on the mode of origin of the Chorion,' from Philos. Trans. 1837.


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Fig. 1, an ovum found in the Fallopian tube of a rabbit the third day after impregnation, magnified forty diameters.—Fig. 2, the ovum of the frog when recently laid, magnified two diameters.—Fig. 3, the ovum of a water-newt, in which development has commenced, magnified rather more than twice.—Fig. 4, a diagram showing the embryo of the newt after the vitellary membrane has given way, contained only within the cavity of the substance, which is added to the ovum in the oviduct.—Fig. 5, a diagram showing the embryo of the frog still

produced, which occupies the centre of the ovum, and of which each component vesicle contains a colourless, pellucid nucleus, and each nucleus presents a nucleolus. R. W.]

§ 70. *The Ovum in the Uterus to the Formation of the Embryo.*

As soon as the ova have passed from the oviducts or Fallopian tubes and reached the uterus, they begin to undergo the first remarkable changes and to grow with rapidity. The following particulars are given with an especial reference to the ova of the bitch and rabbit, the ova of these animals having been most frequently examined, and in their successive metamorphoses also presenting more numerous analogies to the ovum of man, than those of the ruminants. The ova still contained within the cornua of the uterus are found notably increased in size; here they are from half to three-quarters of a line in diameter, whilst in the ovary they measured no more than from the tenth to the twelfth of a line. It is easy to perceive that the outer coat or chorion expands and becomes thinner; the yolk enlarges and becomes more fluid, whilst the dark granules vanish and larger oil-globules make their appearance; the superficial granular layer of the vitellus at the same time acquires a membranous consistency, and the granules collect in heaps or clusters, which are divided from one another like little islands, and anon collecting in one particular part they form a darker circular spot, which in ova that have attained a line in size may be distinguished as a point with the naked eye (fig. LXVIII. *A*, *B*, fig. LXX. *A*, *B*). This macula or spot consists of a larger aggregation of granules, which rises slightly

surrounded by the vitellary membrane, as well as the gelatinous substance, which is added to the ovum in the oviduct.—Fig. 6, an ovum found in the horn of the uterus of a rabbit seven days after impregnation, magnified forty diameters.

Fig. LXV.

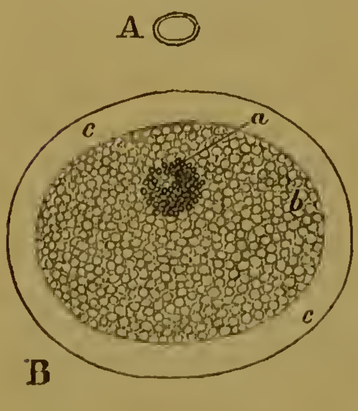

Fig. LXV. An ovum from the uterus, but still unattached; *A* of the natural size, *B* magnified; fourteen days after the first, eleven days after the last approach of the male; the granular rings have disappeared; the granular spot *a* has increased in dimensions; *b*, the vitellus; *c*, the chorion, which has become much thinner apparently, from the imbibition of moisture, is now at a considerable distance from the vitellus.

as a disc above the general level, from its being somewhat thicker than the rest of the membrane; it by and by becomes a little clearer in the centre, whilst the granules are clustered more closely ring-wise in the circumference (fig. LXV. *A* and *B*, more highly magnified fig. LXVI. *b*). The granules of this disc appear plainly to be cells having a small nucleus in the centre (fig. LXVI. *a*). The double membrane with which these small ova are enveloped, is rendered very distinct by putting them for a few seconds in water; here the outer coat (fig LXV. *B. c*), which is perfectly transparent and without visible structure, separates quickly from the inner coat which surrounds the yolk and supports the granular macula (fig. LXV. *B*, *b*.). The external membrane is the future CHORION, the inner the BLASTODERMA, which has already enveloped the entire vitellus, and even earlier perhaps surrounded this part as a continuous granular layer (vide annot. 62 to § 20); in the bird, on the contrary, (§ 47) the blastoderma only occupies a small part of the superficies of the yolk as a disc-like granular stratum. The space between these two coats (fig. LXV. between *b* and *c*), is in all probability filled with a thin stratum of albumen, which the ovum has attracted in the tube and beginning of the uterus, and which by imbibing water has swollen, and thus occasioned a greater separation between the two membranes of the ovum. The granular spot is the point from which the formation of the embryo begins, and which has therefore by some observers been called the *embryonic* spot. Whether the membrane which we have hitherto seen as the outermost continues so, resolving itself into the shaggy chorion, or there is another delicate membrane thrown around this as the

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Fig. LXVI.

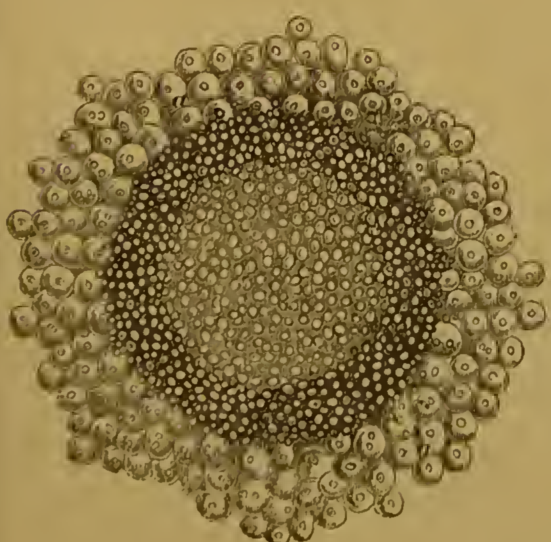


Fig. LXVI. The granular spot of the ovum last figured, magnified. It is seen to consist of cells with nuclei, *a*, in the circumference, and in the inner part of granulations, which are observed of different sizes and densities. These granules and cells together, form the rudiments of the germinal membrane (*blastoderma*).

true outer covering of the ovum—the exochorion—as some maintain, is doubtful. The former appears the more probable view. The ova still lie free and unconnected in the uterus; from having been round they now become oval in their form[138].

[138] I have made the above statements entirely from my own observations on the ova of rabbits and dogs. The figures of the ovum of the dog as given by Prevost and Dumas in the *Ann. des Sc. Nat.* t. iii. pl. 5, may be referred to in this place; as also my own representations of the ova of the rabbit and dog in my Contributions (*Beiträge*, &c.) tab. I. fig. 9, and likewise the descriptions and drawings of Coste (*Embryogenie*, pl. IV. V. VIII.) of the ova of the dog, sheep, and rabbit. It is Coste who calls the granular spot from which the formation of the embryo begins the embryonic spot (*tache embryonnaire*); Baer was before Coste in all requisite observations on this part in his *De Ovi Mammal. et Hom. Genesi*, p. 7—11. More recently Baer has given more extended remarks on the same subject, which in the main agree with all I have myself seen, *Entwickelungsgeschichte*, ii. p. 184. Baer, however, seems inclined to recognize the addition of a particular membrane, the analogue of the shell membrane of the bird's egg—Burdach's Exochorion—to the ovum of the sow and sheep: this membrane, he imagines, is added in the uterus, and an albuminous deposit thrown over it: this formation occurs in the sow on the thirteenth day, an epoch at which the ovum with its vitellus in this animal has become much elongated and filiform. Nothing analogous was observed in dogs and rabbits, and he is still doubtful as regards these animals whether he should admit a new formation, or allow of a metamorphosis of the earlier chorion [thick transparent membrane, zona pellucida] into the outer membrane of the more advanced ovum, the proper shaggy chorion (loc. cit. p. 187). From all that I have myself seen in earlier ova from the uterus, I must conclude that there is no new chorion formed; a conclusion with which the researches of Bischoff accord completely, and of which I am happy to be able to add an account from a manuscript communication of the author. "I have traced the ova," says Dr. Bischoff, "from their first entrance into the uterus from the tubes, quite high in the points of the cornua, to their attachment in their several resting-places. In one instance I found the ova still

Fig. LXVII.

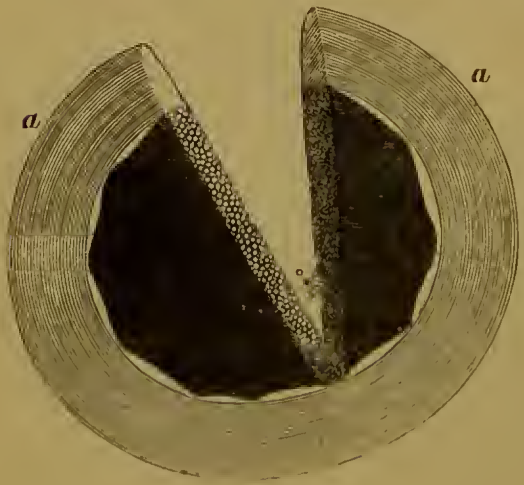


Fig. LXVII. Fecundated ovum of the bitch removed from the upper end of the uterus. The ovum has been flattened and split with a needle; the vitellus is polyhedrous, and shows an angular outline; its contents do not escape: *a*, the chorion or zona pellucida, of great thickness and breadth. The figure is greatly magnified.

First appearance of the Embryo, and farther development of the Ovum, till its attachment to the uterus.

§ 71. As the corroborative and mutually supplementary researches of a host of observers have made us most intimately

very close together, lying quite in the upper pointed part of the uterus, in a bitch which I was given to understand had been impregnated fourteen days before. If this were so, the animal must have been young The ova were still very small, and to the eye in search of them appeared as extremely minute white specks. The most remarkable circumstance I remarked was, that the disc had disappeared, it was not however included by a membrane, but the proper zona pellucida (the chorion, v. Annot. 59) still surrounded the ovum externally. The ovum, and particularly the zona, had increased in diameter (fig. LXVII. *a*). One of the more perfect ovarian ova measured the 0,0072 of a Parisian inch in extreme diameter, the zona included ; the vitellus itself the 0,0056, the thickness of the zona being the 0,0005 of the same inch. The fecundated ovum in its extreme diameter, including the zona, measured from the 0,0082 to 0,0083, the vitellus itself from the 0,0055 to 0,0063, the zona in thickness the 0,0009 of a Paris inch. The separation of the yolk from the inner surface of the zona was more conspicuous now than it appeared subsequently, and now I thought I could no longer doubt of the presence of a fine enveloping membrane. The vitellus was of an irregular shape in all ; in one this was particularly remarkable, a portion of it appearing to be pinched off from the rest ; in another it looked almost as if it were eight-cornered ; the vitellus, however, was still uniformly dark and opaque. The ovum generally was very consistent and elastic, for I could press it quite flat without bursting it ; by which, of course, it increased very much in diameter. (Fig. LXVII. exhibits an ovum split with a needle, the yolk-granules not escaping, and the yolk itself angular in the periphery.) The observations I had occasion to make on another bitch which had been eleven days in my possession, and had not during that time suffered any dog to approach her, although she continued strongly in heat, corresponded closely with what is related above. The ova on the two sides showed a decided diversity in their conditions. On the left side there were two which plainly were referable to ova in the earlier period, save that they were both somewhat oval, and that in the one the vitellus had connected itself entirely with the one side of the zona. These two ova were near the middle of the left cornu, close to one another. In the right cornu there was one ovum obviously farther advanced ; it lay as low as the lower third of the horn, was completely transparent, quite round, and about the third of a line in diameter. With my unaided eye I could perceive a white point or speck. This, under a powerful lens, had an extremely beautiful appearance. The vitelline granules had all, as it seemed, attached themselves in distinct rings to the inner aspect of the very delicate external covering ; at one part there was a small agglomeration of granules (similar to that represented in fig. LXVIII. *B*, *c*). More closely examined, it appeared that to the outer envelope there was an inner one intimately applied, within or upon which the granular ring lay. This inner envelope showed less disposition to separate from the outer one when put into water than in more advanced ova. The ova in the right and left cornua uteri in this instance differed so much in their state of development, that I had no difficulty in detecting ova in another

acquainted with the ovum of the dog, a sketch of its evolution will, I imagine, be found very much in its place here. In all essential

bitch in a stage intermediate between them. The separation and arrangement of the vitelline granules in rings here appeared to have taken place from the middle towards the superficies. The rings ran very close to one another and were broad; the ova much smaller than the one on the right side in the preceding case, although larger than those of the left side. As they were almost completely transparent, the greatest attention was necessary to discover them in the uterus: in one point I also remarked an agglomeration of granules in this instance as in the former. When the ova had lain for a short while in water, they altered very much in shape; the particular aggregations of the vitelline granules were lost, and they collected again into a dark but very irregularly-formed mass. Here, again, I could not be quite certain that I saw any inner envelope." Instead of the drawings first sent to me by Dr. Bischoff as illustrative of the above particulars, I have given in figs. LXVIII. and LXX. drawings of a couple of ova communicated to me more recently, and with the following remarks appended:—" I believe I can now give you some particulars bearing on the formation of the blastoderma or germinal membrane. I have lately examined two bitches, in which the ova had just reached the uterus from the tubes, but very evidently were not all in the same stage of development. The ova appeared as small vesicles, clear as globules of water, with a scarcely-perceptible white speck on one side, from the 0,0125 to the 0,0150 of a Paris inch in size. Under the microscope the zona appeared already to have become considerably thinner (fig. LXVIII. *B*, *a*); the inner superficies was occupied with granular rings, among which one larger, darker granular spot (fig. LXVIII. *A*, *c*), and several smaller (*d*) were conspicuous. With the greatest attention I remarked in several of these ova certain

Fig LXVIII.

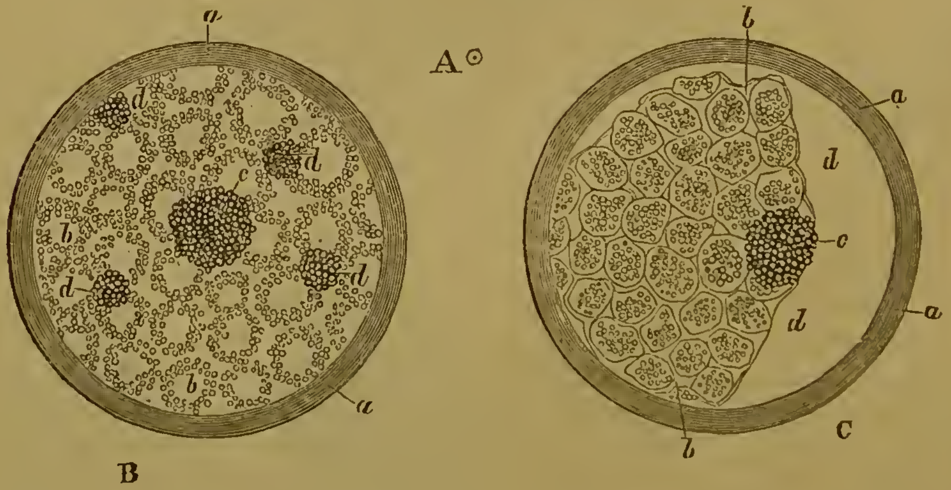


Fig. LXVIII. Ovum of the dog, further advanced than the last. *A*, natural dimensions; *B*, magnified view; *a*, chorion; *b*, *b*, *b*, vitellary granules forming rings; *c*, macula embryonic spot (*tache embryonnaire, Coste*); *d*, *d*, *d*, smaller dark heaps of granules interspersed among the vitellary granular collections. *C*, the same ovum altered through the imbibition of water; the vitellus *b*, *b*, has shrunk, and a free space, *d*, *d*, has arisen; *a*, the chorion; *c*, the embryonic macula.

points that of the rabbit, and even of the sheep, which, after the dog, are best known to us, will be found to correspond. The period

very delicate lines, drawn in circles around and including the granular rings. In water a delicate inner covering (fig. LXVIII. *B, c*) was detached from the outer one (*a*) as in the ova formerly studied; the inner vesicle shrunk together, so that an empty space (*d, d*) was produced between the two; along with this the regular arrangement of the yolk-granules disappeared. It required great pains to succeed in tearing the outer covering with fine needles, and the inner one partially, so as to obtain a view of the dark spot by itself and without intervention. I now saw clearly that even in these ova (as in those of greater age represented figs. LXV and LXVI.) the outer covering was entirely composed of vesicles or cells in close apposition with one another, and containing in their interior larger or smaller numbers of granules, which lost their regular arrangement in water and exhibited molecular motions. By this means, and also by rolling, I satisfied myself that the granules were not attached externally to, but contained within, the cells; I could discover no other more remote nucleus to any of these cells. I also found cells in the dark spot, and here they contained still larger quantities of granules, and lay one upon another. Between these cells containing granules, numbers of other smaller dark globules were perceived, composed of clusters of cohering yolk-granules, but surrounded by no particular covering; as these could be distinguished agglomerated, it was impossible that

Fig. LXIX.

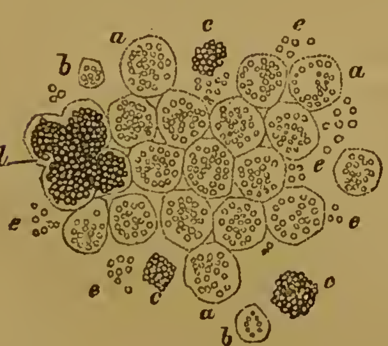


Fig. LXIX. Granular cells of the germinal membrane of the last figure, more highly magnified. *a*, Larger cells; *b*, smaller cells; *c*, granular globules without cells; *d*, cells of the embryonic spot; *e*, granules from ruptured cells.

Fig. LXX.

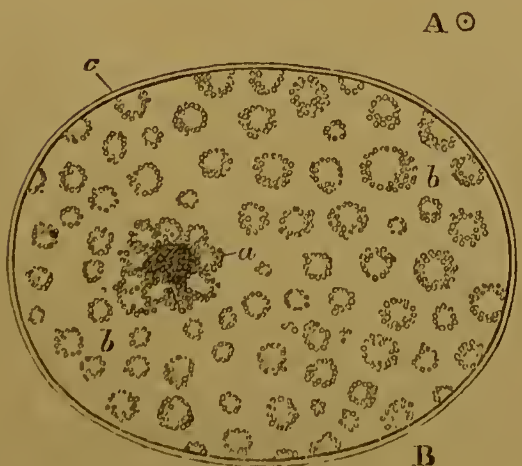


Fig. LXX. Ovum of the dog, from the uterus, but as yet unconnected with it, fourteen days after the first and eleven days after the second access of the male. *A*, the ovum of its natural size; *B*, the ovum seen under the lens. The rings of vitellary granules have disappeared; the dark granular mass *a*, the embryonic spot, has enlarged; *b*, the vitellus; *c*, the chorion, which has become comparatively much thinner, and probably from the imbibition of fluid appears at some considerable distance from the yolk.

to which the various stages in the development are referred is usually that of the last intercourse; but these, as has been already

they could have been cells, the investing membrane of which had been accidentally torn; for as soon as any true cell was ruptured, the included granules were immediately dispersed in the surrounding water. (Vide fig. LXIX. which gives a more highly magnified view of the cells of figure LXVIII.) We now approach the form described by you (*Beitr. z. Gesch. d. Zeug.* tab. I. fig. 8 and 9.) and others, of which I therefore only send the representation (fig. LXV and LXX.). As the ovum continues to grow continually by the absorption of fluid, the granular rings of the second inner covering, which is constantly becoming more conspicuous, separate more and more from one another, and the ovum assumes an oval form. Although the ovum has now attained its resting-place, still it is by no means firmly attached: at this stage the ovum is more readily detected and easily observed. I have paid the greatest attention to the granular cumulus; it unquestionably lies within the second envelope. Upon one occasion I thought I had detected the germinal vesicle in it, but I soon satisfied myself that this was not the case. The granular cumulus consists entirely of an aggregation of granules, which leave a depression in the middle, around which the mass is disposed like a wall. Vide fig. LXV. *A* and *B*, and fig. LXX. *A*, *B*. The former is an ovum fourteen days after the first intercourse known to me, eleven days after the last; *A* is the natural size, *B* the same object as seen under the simple lens; the granular rings have disappeared; in their stead, and within the inner envelope, under a power of 250 (fig. LXVI.), nothing but cells are seen, and these so closely set together that they mostly show as six-sided figures. In the centres of these cells there are small nuclei contained, and in addition and between them an irregular granular matter. Midway between them is the wall-like granular cumulus. The outer envelope of the ovum was extremely fine and delicate. I take it there can be no doubt but that this outer envelope is the attenuated much-distended zona pellucida of the ovarian ovum, which is now known under the name of the chorion. The inner covering is a product of development, but not, as it seems, by any apposition or coalition of the vitelline granules, for these are still present and conspicuous in the granular rings after the formation of the membrane. As it is in this that the granular cumulus is contained, from which the development of the embryo proceeds, it ought to be called the germ-vesicle—the later umbilical vesicle."—"When I place my earlier in contrast with these my later observations, I imagine the process of the formation of the cells to be as follows:—The yolk-granules first cluster into small globular masses (*nuclei*), which then become surrounded by a cell. With the growth of the cell the granules separate from each other, become grouped into concentric rings, and in their turn form the nuclei of new cells, until at length each yolk-globule becomes surrounded with a cell, and so the blastoderma is engendered, as in fig. LXV and LXVI. where each cell incloses a simple nucleus. In figures LXVIII and LXIX, the cells are still few in number, and consequently there are many granules in each cell; in fig. LXX. the cells are more numerous and the nuclear granules fewer; in figures LXV and LXVI. the cells are still more numerous, and each contains but a single nucleus. Were we to extend this process, the alterations observed in the form of the yolk would be perhaps found to be due to it; all the yolk-granules being inclosed first in

stated, are very variable. On the twelfth, or from that to the sixteenth day, the ovum, which, from its originally rounded, has already assumed an oval form, begins to be drawn out at both poles, and to appear somewhat pointed or lemon-shaped (fig. LXXI.); it is about three lines in length, and half as much in thickness; the external membrane, or chorion, is still smooth; the internal vesicle is oval, and in its middle presents a clear pear-

two, then in four, then in eight cells, and so on, until each at length comes to have its own cell, which coalescing with one another the blastoderma is produced as a preliminary to the appearance of the embryo. These cells are of various sizes; in figs. LXVIII. and LXIX. the greater number measured from the 0,0014 to the 0,0018 of a Paris inch; some, however, no more than the 0,0008 of a Paris inch." These excellent observations of Dr. Bischoff give a clear insight into the earliest formative relations of the germ, and with a few modifications may undoubtedly be applied to the germ of the bird (§ 47 and § 84, where the subject is the histological or structural development), and of the human ovum; they may be viewed as fruits of Schwann's discoveries in regard to the cellular structure of the tissues in both kingdoms of nature. [" In the ovum arrived in the uterus, a layer of vesicles makes its appearance on the whole of the inner surface of the membrane which now invests the yolk. The mulberry-like structure [the embryonic spot] (which had been formed by the successive evolution and aggregation of nucleated cells), then passes from the centre of the yolk to a certain part of that layer (the vesicles of the latter coalescing with those of the former, where the two sets are in contact, to form a membrane—the future amnion), and the interior of the mulberry-like structure is now seen to be occupied by a large vesicle containing a fluid and dark granules. In the centre of the fluid of this vesicle is a spherical body, composed of a substance having a finely-granulous appearance, and containing a cavity filled with a colourless and pellucid fluid. This hollow spherical body seems to be the true germ. The vesicle containing it disappears, and in its place is seen an elliptical depression filled with a pellucid fluid. In the centre of this depression is the germ, still presenting the appearance of a hollow sphere."—" The germ next separates into a central and peripheral portion, both of which, at first appearing granulous, are subsequently found to consist of vesicles. The central portion of the germ occupies the situation of the future brain. From the region, occupied by the germ, there issues a hollow process, which, enlarging, comes to line the inner surface of the ovum or membrane, that enters into the formation of the amnion, and that corresponds to the *serous lamina* of authors, the lining itself representing the incipient state of the subsequent *vascular lamina* of the umbilical vesicle, a lamina continuous with the structure which corresponds to the *area vasculosa* of authors on the bird. There does not occur in the mammiferous ovum any such phenomenon as the splitting of a germinal membrane into the so-called *serous*, *vascular*, and *mucous laminæ*. Nor is there any structure entitled to be denominated a *germinal membrane;* for it is not a previously existing membrane, which originates the germ, but it is the previously existing germ, which, by means of a hollow process, originates a structure, having the appearance of a membrane. From M. Barry. R. W.]

shaped space, the GERMINAL AREA (fig. LXXI. *B*, *c*), which is bounded externally by the vascular area, with its still large (and more conspicuous) granules; the PRIMITIVE STREAK or TRACE is at the same time discovered (fig. LXXI. *B*, *c*, fig. LXXII. *a*); a little later, in ova of four lines in length, which are completely lemon-shaped in their outline, the transparent germinal area is longer and more fiddle-shaped, the chorda dorsalis with the enlargement towards its cranial end, and the two laminæ dorsales, are all expressed; the dorsal laminæ unite first in the middle line of the future back, but before this happens the vertebral laminæ have made their appearance as four-cornered dark spots; this takes place on the seventeenth or eighteenth day, when the embryo is about two lines in length. After the coalition of the dorsal laminæ, the embryo, which lies with its long axis in the line of the transverse axis of the elongated ovum and uterus, begins to bend in upon itself, the head first, and then the tail tending downwards; at this epoch it is also becoming more and more distinct from the blastoderma, which has now grown around the whole yolk as an elongated bladder or vesicle, and separated gradually as the umbilical vesicle from the intestinal canal already in the course of evolution, but is still in free communication with the boat-shaped abdominal cavity of the embryo, and is covered with a very abundant network of vessels. At this time—about the twentieth day—the ovum (fig. LXXIII.) is ten lines in length, the embryo (fig. LXXIII. *a*) somewhat more than three. The chorion has pushed forth small cylindrical shaggy processes or villi, but it is still smooth and transparent at that part where the embryo lies

FIG. LXXI.

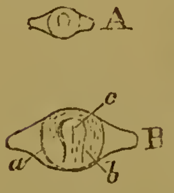


Fig. LXXI.—An ovum from a bitch the seventeenth day after the last access of the male; the chorion is seen already to present the figure of a lemon. *A*, the ovum of the natural size; *B*, the ovum slightly magnified; *a*, the chorion; *b*, vitellus, upon the surface of which, and appearing through the membranes, the pear-shaped area pellucida, and, unless I am mistaken, the nota primitiva or primary streak, *c*, are seen.

FIG. LXXII.

Fig. LXXII.—Ovum of the bitch, after Prevost and Dumas (*Ann. des Sc. Nat.* 1825, t. iii. tab. 5). The primary streak, or perhaps the chorda dorsalis, is perceived in the middle of the pyriform area pellucida, which is surrounded by the more egg-shaped area vasculosa.

under it upon the blastoderma and umbilical vesicle (fig. LXXIV. *A*), although at a later period it also produces villi in this situation; at both poles, however, it always remains smooth and without villi; the vessels are seen proceeding from the embryo to the blastoderma as the omphalo-mesenteric trunks (fig. LXXIV. *c, c, c*) and forming a rete or network upon the umbilical vesicle. The dorsal laminæ have coalesced through their entire length; posteriorly (fig. LXXIV. *B. d*) they still continue a little way apart, so that here a lancet-shaped space remains, as in the chick (fig. XXXVI. at *f*); the brain and spinal cord are formed, the former appearing divided into many vesicles or cells; the number of vertebral laminæ has increased; the eye and the ear are indicated. The abdominal laminæ have been sent off from the dorsal laminæ, and converge to effect the closure of the cavity of the body; three branchial fissures and the same number of arches are obvious (fig. LXXV. *b*,

Fig. LXXIII.

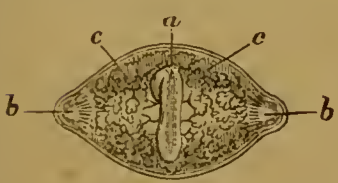


Fig. LXXIII.—Ovum of the bitch twenty-three days from the last access of the male. The chorion, *c, c*, has already shot forth little villi, which, however, are wanting at either end, *b, b*, of the ovum, and also over the place where the embryo is situated. Object of the natural size.

Fig. LXXIV.

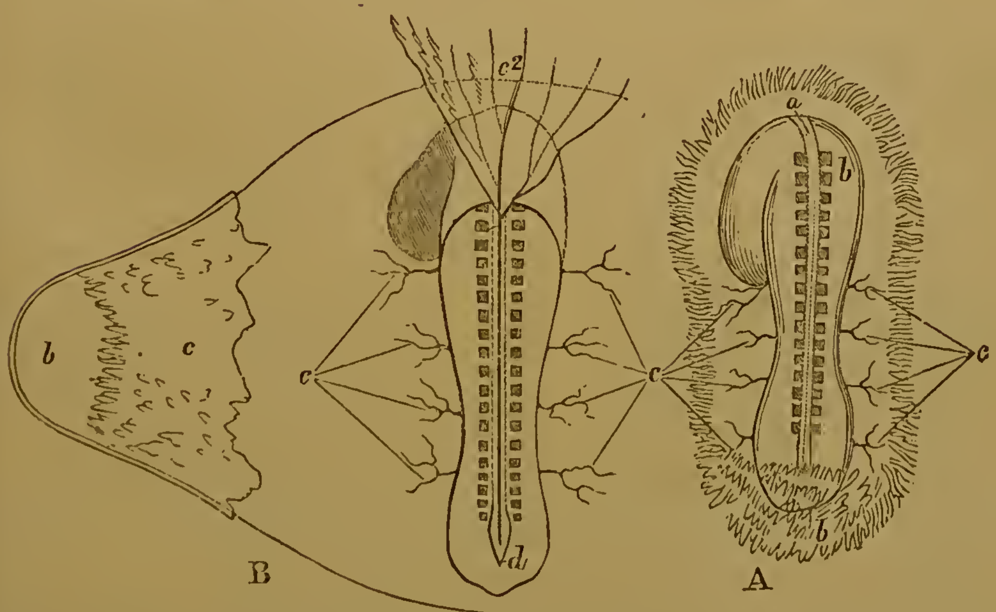


Fig. LXXIV.—*A* and *B*, magnified views of portions of the same ovum and embryo. *B*, c^2, is the chorion removed from the embryo and reflected upwards. *c, c, c, c, A* and *B*, the arteries of the germinal membrane; *a, A*, chorda dorsalis; *d, B*, inferior lancet-shaped extremity of the spinal marrow. Vide fig. XXXVI. and compare the embryo of the fowl with this.

fig. LXXVII. *c, c, c*); the upper layer of the serous lamina has been raised to form a cranial and caudal involucrum, and originates an amnion, which in the first instance surrounds the embryo very closely (fig. LXXVI.) as a serous envelope. The heart and vessels

Fig. LXXV.

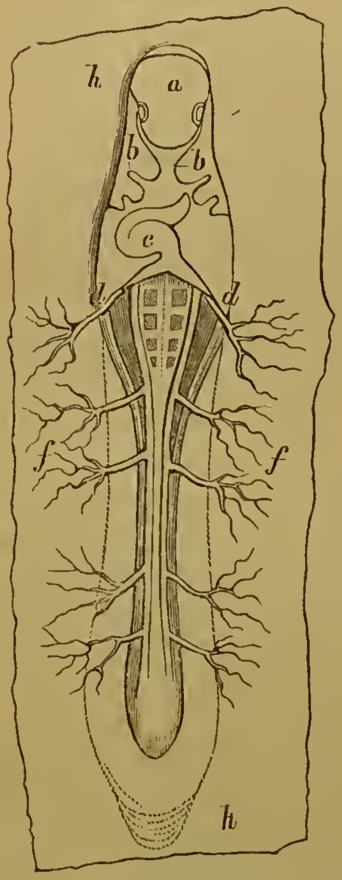


Fig. LXXV.—The same embryo still more highly magnified, and seen from the abdominal aspect: *a*, vertex; *b, b*, branchiæ; *c*, heart, appearing as a contorted pouch; *d, d*, veins of the germinal membrane; *f, f*, arteries of the same, springing from the two aortas; *h, h*, germinal membrane.

Fig. LXXVI.

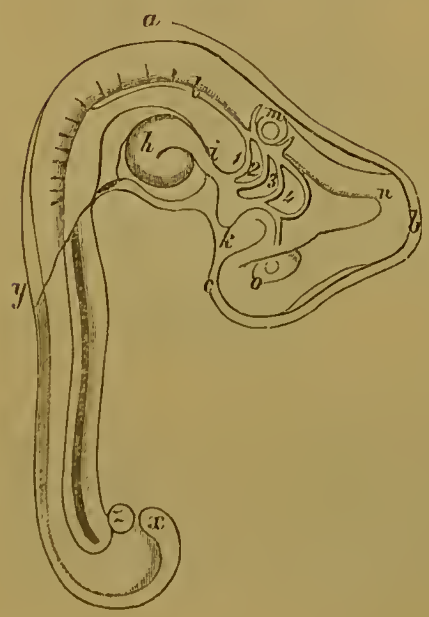


Fig. LXXVI.—Embryo of the dog of the third week, magnified; after Baer (*De Ovi Mammal. Genesi*, vii.): *a, b, c, y*, the amnion; at the curve of the tail, *x*, the allantois, *z*, is seen as a minute vesicle; *h*, the heart, from which springs the aorta, *i*, with its bulbous enlargement, *k*, from which arise the four arteries of the branchial arches, 1, 2, 3, 4, that afterwards unite and form the abdominal aorta, *l*; *m*, the auditory organ; *n*, the corpora quadrigemina; *o*, the eye.

have now formed in the vascular lamina; the heart in the first instance appears as a twisted canal (fig. LXXVI. *h*, fig. LXXV. *c*, and fig. LXXVII. *d*); at the under side, where the future atrium is formed, it receives two omphalo-mesenteric veins (fig. LXXV. *d*, *d*), and in the situation of the future bulbus aortæ it divides into four vascular arches (fig. LXXVI. 1, 2, 3, 4) which first unite into the aorta, again divide, run down near the vertebral column, and give off transverse branches, the arteriæ omphalo-mesentericæ (fig. LXXV. *f*, *f*), which, with the corresponding veins of the same denomination, form a network over the surface of the blastoderma and umbilical vesicle. The allantois springs from the inferior end of the intestinal canal, in the shape of a little vesicle (fig. LXXVI. *z*). The yolk becomes more and more fluid every day within the umbilical vesicle, and contains numerous drops of oil. On the inner aspect of the uterus the vessels enlarge in size and increase in number, and an exudation ensues which acquires a membranous consistence; this is the decidua, which consists for the most part of epithelial cells, connected by means of an albuminous matter and vessels; into this lining, or covering, as the uterus or ovum is considered, the villi of the chorion shoot and grow. The allantois increases rapidly in size, soon grows around or encircles the whole embryo with the umbilical vesicle, carries two arteries from the aorta with it, and is composed of an external vascular, and an internal mucous layer; it is in contact with the chorion almost in the entire circumference of the ovum, with the exception of the two poles, which are without villi, and thus forms the endochorion, or inner layer of the chorion; its vessels also grow into the cylindrical villi, the blood of the arteries that penetrate these returning by corresponding veins, which collect into a trunk that terminates in the inferior vena cava; it is thus that the umbilical vessels are produced, when the particular vascular system of the germinal membrane and umbilical vesicle becomes obliterated.

Fig. LXXVII.

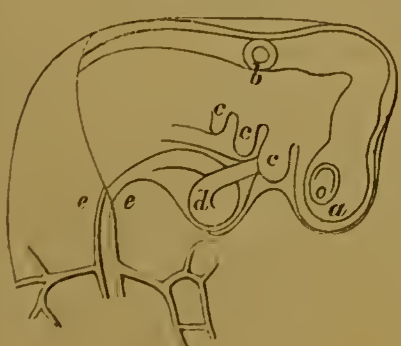


Fig. LXXVII.—Same embryo as in fig. LXXV. from the side: *a*, eye; *b*, ear; *c*, *c*, *c*, branchiæ; *d*, heart; *e*, *e*, trunk of the aorta Compare with this figure, that of Baer, fig. LXXVI., and those of the embryos of the fowl, already given (figs. LXXIII.—LXXV. and this, are after original drawings by Bischoff.)

A placenta—a mass formed of the decidua and the uterine vessels which grow into it on the one hand, and of the umbilical vessels of the embryo on the other, these two systems of vessels not communicating together, however,—surrounds the embryo, at a later period, in the form of a belt. The chorion soon gives way at both poles of the ovum, and the umbilical vesicle escapes through the rent, and forms a hernial sac on either side, so that the ovum now assumes a cylindrical shape. In the fourth week the branchial fissures are closed (fig. LXXVIII.), the extremities have budded as little flattened offsets from the abdominal laminæ (*n*, *o*); the heart (*a*) has now acquired its different parts; the intestine is drawn out towards the umbilical vesicle, as a fine continually decreasing and finally filiform canal (*g*); the lungs (*c*) and the liver (*d*), originally offsets from the intestine, have now become distinctly separated from it; the Wolffian bodies, or false kidneys (*k*, *k*), occupy the rest of the abdominal cavity lengthwise, and now appear as two symmetrical bodies placed on either side of the vertebral column; there is still no visible trace of the kidneys and sexual organs; the tail (*p*) is already well developed[139].

139 The account of the development of the chick during the first five days (§ 49—§ 59), and the figures annexed, ought to be contrasted, step by step, with the details just given. In illustration of these the observations of Bischoff (vide his MS. explanations of figs. LXXIII. LXXIV. LXXV. and LXXVII. in notes to § 70), and the researches of Prevost and Dumas (*Ann. des Sc. Nat.* iii.), of Baer (*De Ovi Mam. et Hom. Gen. et Entwickelungsgeschichte*, ii. p. 213), of Gurlt (*Manual of Physiology of our Domestic Mammalia*, 1837), of Coste (*Embryogénie*, i. 395), of Bojanus (*in Nov. Act. Acad. Nat. Cur.* x. p. 141), and myself, are brought to a focus, as it were, and displayed in these figures (figs. LI. to LXXXIII.), the engravings being either from original drawings, or copied after the writers mentioned. These figures will, I trust, satisfactorily illustrate the very difficult

Fig. LXXVIII.

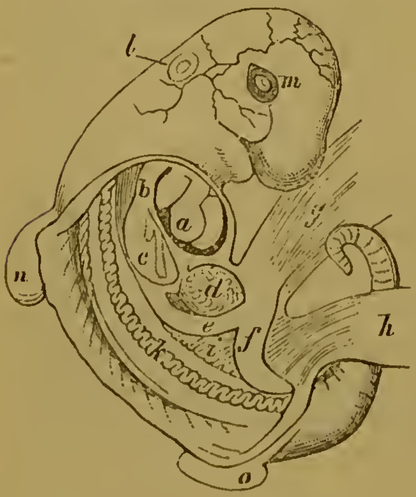


Fig. LXXVIII.— Embryo of the dog, after Coste (*Embryogénie comparée*, t. iv. f. 9), presumed to be twenty-four days old, magnified three times: *a*, heart; *b*, windpipe; *c*, lung; *d*, liver; *e*,*f*, the two portions of intestine which are in communication, at *g*, with the umbilical vesicle; *h*, allantois; *i*, mesentery; *k*, *k*, corpora Wolffiana; *n*, anterior extremity; *o*, posterior extremity.

points in the early stages of development among the mammalia. The form intermediate between those represented figs. LXV. and LXXI. appears to have been observed by Coste (*Embryogenie*, pl. vi. fig. 3), but his figure is not sufficiently decided, and is therefore not made use of. I have observed in the rabbit, that the germinal membrane becomes clearer at the dark spot—the embryonic spot, and first shows a round transparent germinal area. In the dog the ovum appears to pass very soon from the round or oval, into the ellipsoidal and lemon form; I observed it thus, for instance, in the ovum, represented fig. LXXI. (seventeenth day), in which the germinal area has already become pyriform, and the primitive streak appears to be formed. Prevost and Dumas represent the ovum of this period

Fig. LXXIX.

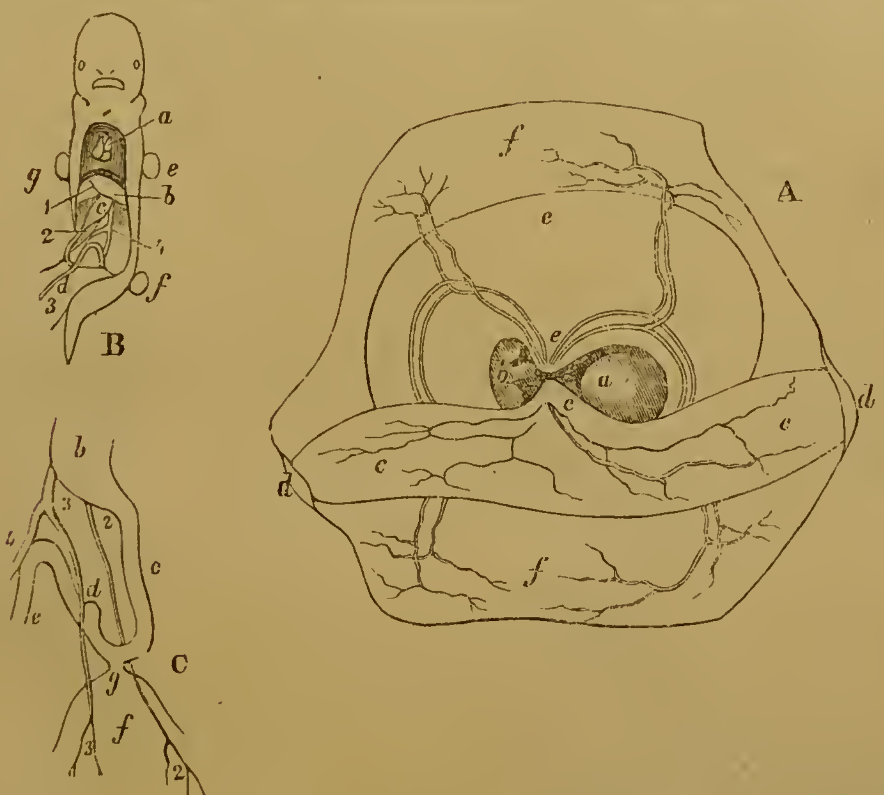


Fig. LXXIX.—Embryo of the dog still farther advanced, after Bojanus (*Nov. Act. Acad. Leopold.* &c. vol. x. p. 140). The embryo is presumed to be of the twenty-fourth day by the writer. *A*, the embryo included in the amnion; *a*, head; *b*, tail; *c*, *c*, *c*, the umbilical vesicle, become of great length, with its vessels; it is covered at its two extremities, *d*, *d*, by the chorion, *f*, *f*, which is laid open; *e*, *e*, allantois, with its vessels. *B*, the embryo of the natural size, from the abdominal aspect; *a*, heart; *b*, liver; *c*, stomach; *d*, stem or duct of the allantois, called brachus; *e*, *g*, anterior, *f*, posterior extremities; 1, diaphragm; 2, cepatic vein divided; 3, omphalo-mesenteric vein; 3, omphalo-mesenteric artery; 4, descending aorta. *C*, intestinal and omphalo-meseraic vessels, magnified; *b*, stomach; *c*, superior piece of intestine; *d*, cœcum; *e*, rectum; *f*, umbilical vesicle, communicating, at *g*, with the intestine; 2, omphalo-mesenteric vein; 3, omphalo-mesenteric artery, proceeding from the aorta, 4. Compare with this figure that of the human embryo of six weeks.

as pyriform (l. c. tab. v. fig. 4), as if one pole only had first been drawn out, a circumstance which I have never observed, and which is perhaps abnormal. The representation of the next stage in the development (fig. LXXII.) is copied from Prevost and Dumas; here the germinal area is already somewhat fiddle-shaped; I hold the streak here to be the chorda dorsalis. Then follow the figures from Bischoff, figs. LXXIII. LXXIV. LXXV. and LXXVII. the ovum being at this time in the twenty-third day. The embryo of about three weeks, given by Baer, in fig. vii. of his *De Ovi Mam. &c. Genesi* (copied in our fig. LXXVI.), is evidently very nearly at the same period of its evolution; the ovum, the figure of which, after Coste, is copied in our fig. LXXVIII. is certainly farther advanced; apparently it has reached the twenty-fourth day. We have next the very clear and carefully drawn figure of Bojanus, of an ovum and embryo of the dog of the twenty-fourth day, which is copied in our fig. LXXIX. *A, B, C.* For further illustration of the subject, and by way of comparison, I have added figures of the embryos of different animals to the close of this period, which may be assumed to correspond, as nearly as possible, to the first four weeks of the human embryo. Fig. LXXXI. is the embryo of a rabbit; fig. LXXXII. that of a sheep, after Coste. The two embryos of the mole, fig. LXXX. *A* and *B*, are about as far advanced as the most forward embryo of the dog given in fig. LXXIX. and

Fig. LXXX.

Fig. LXXX.—Embryo of the common mole (*Talpa Europæa*) three lines in length, drawn under the simple lens: *A*, the embryo entire; *B*, the embryo with the abdomen laid open; *a*, the chorion; *b*, pedicle of the allantois and umbilical vessels; *c*, umbilical vesicle and its duct; the omphalo-mesenteric duct, *d*; *e*, gastric portion of the intestine; *f*, intestinum rectum; *g*, the small but distinctly-marked eye; *h*, branchial arches disappearing; *i*, auditory vesicle; *k*, anterior, and, *l*, posterior extremity; *m*, Wolffian bodies of the left, *n*, of the right side; *o*, the still simple rudimentary lung sessile on the trachea, *p*; *q*, ventricle, and *r*, atrium of the heart. The several divisions of the brain, the nasal aperture, the mouth, &c. are depicted in *A*.

Researches on the human Embryo in the earliest periods.

§ 72. Good descriptions and representations of the human embryo, within the first month from conception, are very scarce[140];

the smallest human embryo, figs. LXXXIV. and LXXXV. In fig. LVII. the embryo of a lizard, with the branchial fissures closing, and the extremities budding forth, is given for the sake of comparison; the correspondence in point of appearance between the embryos of birds and mammalia of the same periods is very obvious.

[140] Among the many descriptions and figures that have been given of ova of the first month, I have scarcely met with one or two that seem calculated to convey correct ideas of the state of the development at this period. By much the clearest and most beautiful representations with which I am acquainted, are those given in figs. LXXXV. and LXXXVI., and referred to in the text as types of the development of the embryo at their respective periods,—the third and the fourth

Fig. LXXXI.

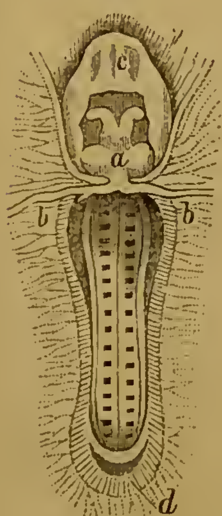


Fig. LXXXI.—Magnified embryo of the rabbit, after Coste (*Embryogénie,* pl. vii. fig. 4): the abdomen is still widely open, the vertebral column shining through; *a,* the heart, receiving the veins, *b, b,* of the germinal membrane; *c,* head; *d,* tail.

Fig. LXXXII.

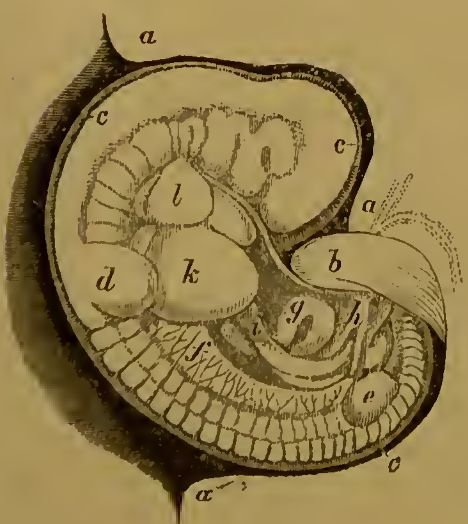


Fig. LXXXII.—Embryo of the sheep of the twenty-fourth day, magnified four diameters, after Coste (*Embryogénie,* pl. vii.): the allantois, *a, a, a,* is only represented as it arises; *b,* pedicle of the vesicula umbilicalis; *c, c, c,* amnion, still lying very close; *d,* fore, and *e,* hind extremity; *f,* Wolffian body; *g,* noose of intestine; *h,* pedicle of the allantois; *i,* the right vena umbilicalis; *k,* liver; *l,* heart.

N. B. These latter figures, from LXXIII. to LXXXII. are adapted for comparison with those of the human embryo, fig. LXXXIII. et sequent.

it is true indeed that we have many accounts of diseased ova, of monstrous or distorted embryos of this period; but instead of aiding

week. The smaller embryo, which measures but two lines in length (fig. LXXXIV. LXXXV. and LXXXV. *A*), was examined by me so long ago as 1831. The decidua surrounding the ovum presents itself as a bladder closed on every side (fig. LXXXIII.), and was perfectly normal, slightly shaggy externally, and without doubt had been connected by means of its villi with the uterus. The various details, which are given with the greatest fidelity in the figures, represent, as I conceive, the entirely normal development; the embryo, however, from its condition, must have died some short time before abortion took place. The anterior cerebral vesicles and the upper-jaw are proportionally somewhat too large; but these appear to be the only parts that are not thoroughly normal. Very similar to this embryo appears to be the one described by Müller in his *Archiv* for 1834; the ovum and embryo, however, were somewhat larger than mine; the chorion was between seven and eight lines, the embryo two lines and a half, in their long diameters. The umbilical vesicle, a line and a half in length, as in the embryo figured by me, also went quite wide over into the intestine, the place of the future pedicle being only indicated by a slight constriction; the amnion lay immediately and closely upon the embryo. According to Müller, this ovum was either *thirty-four* or *thirty-nine* days old; the latter he holds the more probable age; intercourse had taken place on the 2nd December,—on the 25th, the expected menstrual period was missed. On the 27th, intercourse again took place, and on the 5th of January the ovum was thrown off. I am firmly persuaded, along with Baer, *Entwickelungsgeschichte*, ii. 270, that this ovum was *twenty-one* days old,—from the 5th to the 27th of December, and that the second intercourse detached it. The fœtus described and figured by Müller, in Meckel's *Archiv* for 1830, tab. xi. fig. 11., is of singular beauty and quite normal. I have given a copy of this fœtus in fig. LXXXVI. *A*, of the natural size, *B*, enlarged, and in *C* have added a view of it still surrounded by its membranes, as these must have existed according to the laws of analogy and the numerous observations which I have made on other occasions. My object in this was for the sake of comparison with fig. LXXXV. *A*. All the older representations of embryos at this early period are valueless, partly from want of the requisite attention to detail, and partly from the defective state of knowledge in regard to the import of the several parts and their mutual relations.—Vide a list of such figures in Burdach, *Physiol.* ii. 449. Those of Soemmerring, Pockels, Kieser, Meckel, and Hunter, I regard as being from fœtuses that have either suffered from disease, or are actual monstrosities. By this, I do not mean to say that the study of such abnormal embryos is of no interest in a physiological point of view; on the contrary, many parts often exist quite normal in their formation, though others may be very much the reverse. Baer, for instance (*Entwickel.* ii.), has figured and described many embryos at an early period that are generally monsters; but the intimate knowledge of development possessed by this writer has enabled him to describe things correctly and according to the standard. The writer just quoted has some excellent observations on this subject in *Siebold's Journal*, xiv. 401, with plates. [The reader is further referred to a highly interesting paper by Dr. Allen Thomson, in which descriptions are given of three very early embryos examined by him, in the *Ed. Med. and Surg. Journal*, for

us or advancing our knowledge of the earlier periods of development in the human subject, these accounts are even generally calculated to mislead, and it is therefore well to regard the greater number of them as of no kind of value [141]. Some have said that they had found ova in the tubes, or on their very first entrance into the uterus, and before the separation of the embryo from the germinal membrane [142]; but all statements of this kind yet in existence are in the highest degree unsatisfactory. The smallest ova hitherto observed in the uterus, or thrown off by abortion, which in the present state of knowledge in regard to the history of development can be allowed to be normal in their formation, or even as departing but a little from the rule, have been about three weeks old. Such ova, still surrounded by the decidua (figs. LXXXIII. LXXXIV.

July, 1839. R. B. T. And to an account of a human ovum described by T. Wharton Jones (*Philos. Trans.* 1837), which is probably the earliest that has yet been seen; certainly earlier than either three or four weeks, the period which Mr. Jones, following Dr. M'Kenzie, assigned to it. R. W.]

141 The subject of diseased ova and malformed embryos will be taken up farther on in this work. Meantime, I may say, that after much inquiry I find an effusion of blood into the decidua, on the formation of the reflexa and serotina, to be the primary cause of the death of the embryo in the majority of cases. When this has occurred, ova may still go on increasing for some considerable time, as Meckel remarked, though the embryo makes no further progress;—a fact which accounts for the usual immense disproportion in aborted ova between the size of the envelopes and the little misshapen and sometimes totally wanting embryo. Velpeau has given a collection, and in this point of view a very interesting collection of figures of monstrous ova and embryos.—*Embryologie Humaine*, Paris, 1832. But the views which he and many others have adopted from the study of such abortions, in regard to the allantois, the formation of the amnion, &c., are altogether erroneous.

142 The well-known accounts which we have from Home and Bauer and others, of ova found in the tubes, or at an extremely early period in the uterus, and which Coste has lately referred to and used with so much confidence, I hold to be so uncertain that they are altogether without value to science. The early embryos and ova described by Pockels (*Isis*, 1825), I also believe to be so much altered and so abnormal that they can only be used with the greatest reserve.

Fig. LXXXIII.

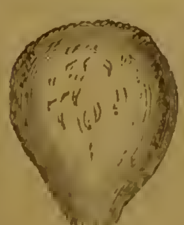


Fig. LXXXIII.—A perfectly normal human ovum of the third week (about twenty-one days old), enclosed in the decidua. Size of nature.

and LXXXV. *A, B*), measure about seven lines in length; in the naked chorion they are about five lines long. The chorion at this time is beset externally with small cylindrical, hollow villi, which either do not penetrate the decidua at all, or do so to a very trifling extent. The embryo itself is two lines long (fig. LXXXIV. the natural size, fig. LXXXV. magnified, fig. LXXXV. *A*, with references, and *B*, cross-lines to indicate the natural size). It is plainly surrounded by an amnion (fig. LXXXV. *A, c*), which lies loosely but still pretty closely about it, and obviously proceeds from the abdominal laminæ. The embryo is curved (in the figure it is re-

Fig. XXXIV.

Fig. LXXXIV.—The same ovum laid open; the embryo, about two lines long, closely surrounded by the amnion, is seen through the division in the chorion.

Fig. LXXXV.

presented as brought forward from or out of the amnion); and presents anterior cerebral vesicles or hemispheres (k^1) pretty well developed (in the embryo figured they are perhaps abnormally large), and considerable corpora quadrigemina (k^2) immediately behind them; there is the distinct appearance of an eye (r), and a rounded offset from the medulla oblongata indicates the acoustic vesicle (i); several branchial arches and fissures are also conspicuous, the last of them, however, not yet completely formed. (In the embryo here particularly referred to for example, the oral aperture may be observed before the lower jaw (h), followed by two branchial fissures; the third branchial arch succeeding the last of the fissures is not yet completely detached.) The anterior (l) and the posterior (m) extremities are curved leaf-like processes, still of

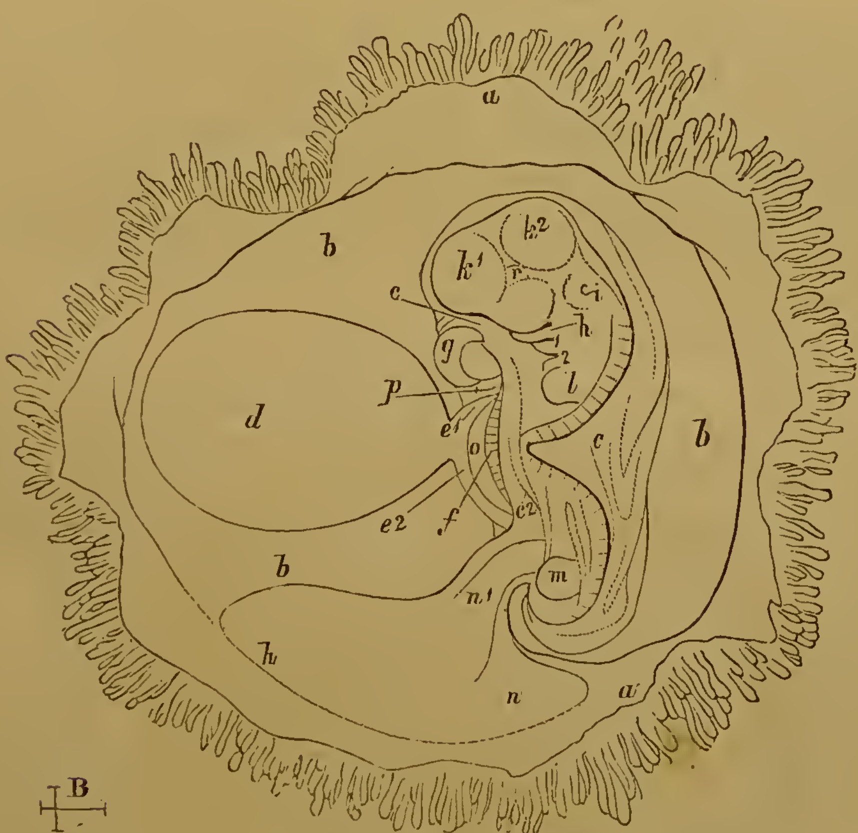


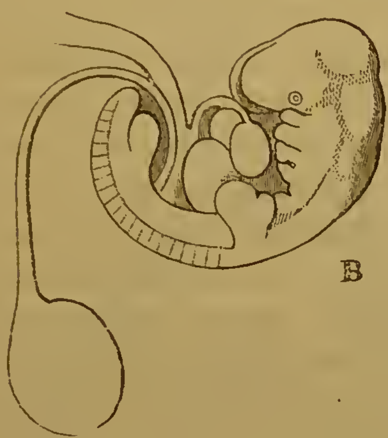
Fig. LXXXV.—The same same ovum magnified; the whole of the parts designed from nature.—*a*, *a*, Chorion laid open and reflected; *b*, *b*, *b*, albuminous space betwixt the amnion and chorion; *c*, amnion, which is still open from c^1, in front, to c^2, behind; *d*, umbilical vesicle, communicating with e^1, the ventricular intestine, and e^2, the rectum; *f*, corpora Wolffiana; *g*, heart; *h*, lower jaw; *i*, ear; k^1, hemispheres; k^2, corpora quadrigemina; *l*, anterior, and *m*, posterior extremity; *n*, *n*, presumed limits of the lamina vasculosa of the allantois; 2^1, lamina mucosa of the allantois; *o*, mesentery; *p*, liver; *r*, eye; 1, 2, two branchial fissures.

very small dimensions. The anterior aspect of the embryo is occupied by the abdomen, at this time a long and pretty wide cleft (from c^1 to c^2), and still completely open, from which the amnion is reflected as the cranial and caudal involucra. In this cleft, but projecting beyond it in the form of a hernia, lies the heart (*g*), already of very large relative dimensions, and consisting of a simple atrium, or auricle and ventricle; behind the heart is seen the liver (*p*); and under the liver the intestine, which is attached by means of a distinct mesentery (*o*). At the part where the small intestine (e^1) and the large intestine (e^2) meet, the canal makes an extensive sweep in the umbilical vesicle (*d*), which is now not much less in size than the entire embryo. On either side of the lamina mesenterica and in contact with the vertebral column a narrow elongated body (*f*) is observed, which exhibits various constrictions, and is composed of short cœca; this is the Wolffian body or primordial kidney. From the lower extremity of the intestine a hollow sac or bladder (n^1), which attaches itself to the chorion (*a*, *a*), and coalesces with its inner surface, is seen protruding: this is the allantois, which presents itself as a broad, flat, well-defined bladder, the limits of which (*h*—*n*) may often be distinguished on the chorion; here therefore the chorion is also split into two laminæ, of which the inner lamina, or *endochorion*, is smooth, the outer, or *exochorion*, villous. The embryo together with the amnion and umbilical vesicle do not occupy the entire cavity of the chorion; there still remains a considerable space (*b*, *b*), which is filled with a delicate filamentous or arachnoidal tissue, occasionally also with an albuminous fluid, or a fluid that strongly resembles the vitreous humour of the eye.

Embryos of the fourth week (fig. LXXXVI. *A*, natural size, *B*, moderately, *C*, highly magnified, and with references to the several parts,) are about three lines and a half in length. The amnion (*c*) now surrounds the embryo as a capacious envelope, and has become closed in front. The corpora quadrigemina (k^2) still form the largest mass of the brain; in front of them lie the hemispheres (k^1); and behind them the cerebellum (k^3). From the medulla oblongata the process for the organ of hearing (*i*) projects conspicuously. In the eye (*r*), the lens is now obvious, and surrounded by the choroid. Behind the lower jaw (*h*) there are now three branchial fissures and three branchial arches, the most posterior of which is not yet fully detached along its hinder margin from the lamina abdominalis. The anterior and posterior extremities (*l*, *m*), have increased in size, and form rounded and

already in some slight degree detached leaflets. The heart (g) and liver (p) are of considerable magnitude; the intestine (e) rises in

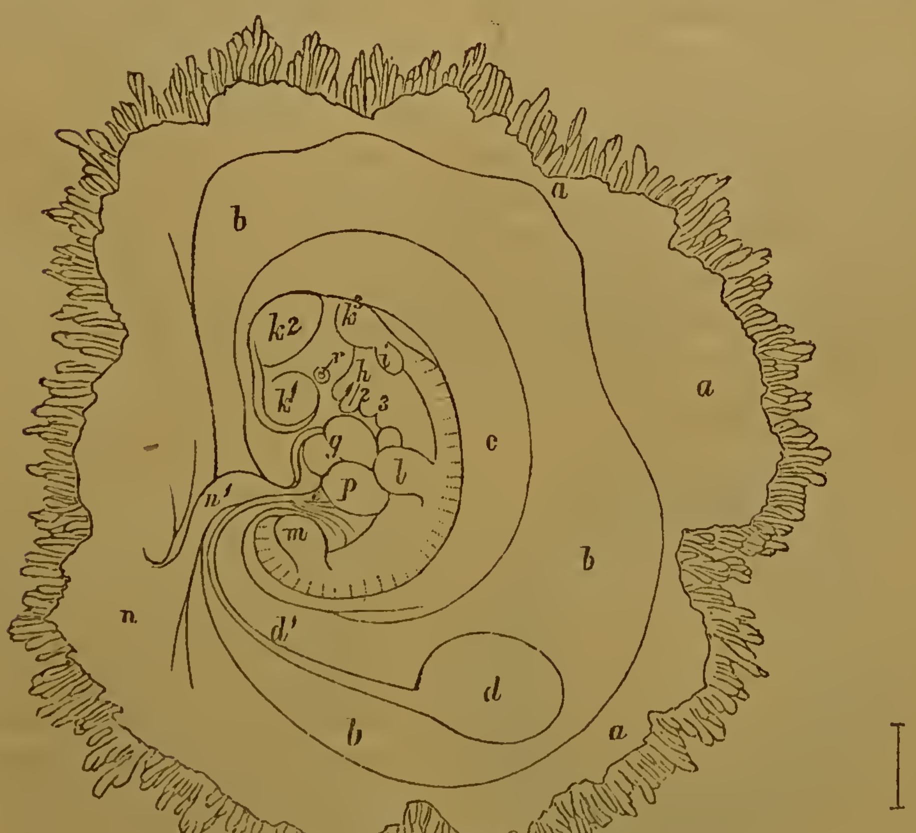
FIG. LXXXVI.



B

Fig. LXXXVI. — A very beautiful embryo figured and described by Jo. Müller, in Meckel's *Archiv*, 1830, tab. xi. *A*, natural size. *B*, magnified view. *C*, view still more highly magnified, with the membranes restored, and references to the several parts. I regard it as about twenty-eight days old. (The references are mostly the same as in the last figure.) *a, a,* Chorion laid open and reflected; *b, b, b,* albuminous space betwixt the amnion and chorion; *c,* amnion; *d,* umbilical vesicle; d^1, pedicle of the umbilical vesicle; *e,* noose of intestine communicating with d^1; *g,* heart; *h,* lower jaw; *i,* ear: *k,* cerebellum; k^1, hemispheres; k^2, corpora quadrigemina; *l,* anterior, and *m,* posterior, extremity; *n,* point where the allantois and chorion have coalesced; n^1, umbilical cord; *p,* liver; *r,* eye; 1, 2, 3, branchial fissures.

A



C

B

sharper loops from the abdomen, and the umbilical vesicle (*d*) is lengthened out into a long, hollow, filiform pedicle (*d'*)—the ductus omphalo-mesentericus; the canal of the allantois (*n'*) has also become longer and narrower, but still expands in the form of a funnel (*n*) towards the chorion (*a*). The chorion internally is smooth; externally the cylindrical short villi with which it is covered have begun to divide, and push forth lateral branches. The space (*b, b*) between the chorion and amnion is still considerable, and filled with the arachnoidal tissue, amid which lies the umbilical vesicle (*d*). In embryos of the third and fourth week, the divisions of the vertebræ are very distinctly marked (as in figs. LXXIII. and LXXIV.) along the posterior aspect, and the caudal vertebræ (ossa coccygis) and forehead are brought close to one another in consequence of the curvature of the embryo. From the account now given, it is obvious that the human embryo of this period bears the greatest resemblance to that of other mammalia both in its general external characters and in the form of its particular internal organs [143].

Human Embryos of the second month.

§ 73. The number of descriptions which we possess of normal human embryos of the second month, when the growth is extremely rapid, is much more considerable. The amnion is now widely separated from the embryo, which it surrounds as a capacious bladder; it incloses the embryo anteriorly, and, investing the pedicle of the allantois and umbilical vesicle, forms the umbilical cord, which connects the embryo with the allantois, and even now is often of greater length than the embryo itself. The villi of the chorion in-

[143] Vide the various delineations of the embryos of mammalia in figs. LXXVI. LXXX. LXXXI. and LXXXII., especially that of the mole, fig. LXXX. *A* and *B*, and also the different ova of the dog, in figs LXXIII. et seq.

Fig. LXXXVII.

Fig. LXXXVII. — Chorion of an ovum of the sixth week. At *a* appears the part which is almost without villi, and which, with the progressive evolution, becomes ever larger and larger; so that the villi seem to collect towards a particular district, and there form the placenta.

crease very rapidly, divide, like a tree, into branches and twigs, which terminate at length in rounded leaflets (fig. LXXXVII.); the villi strike into the decidua, and in one part in particular they are much more numerous and closely set than elsewhere. In the fifth week the embryo, when stretched out, is from five to six lines in length (fig. LXXXVIII. fig. LXXXIX. magnified fig. XC.

Fig. LXXXVIII.

Fig. LXXXVIII. — Aborted ovum, in which all the parts are normal except the decidua reflexa. The decidua vera, *a, a, a*, is seen passing over into the decidua reflexa, *c, c*, which is infiltrated with blood, and much thicker than proper, at the points, *b, b*; *d*, villi of the chorion; *e*, amnion; *f*, a spider's web-like tissue, rendered darker by the action of alcohol in the albuminous interspace; *g*, the umbilical vesicle.

A); the extremities are larger, and project more; behind the terminal rounded hand-shaped portion, a second appears; the head is considerable, the cranial portion in particular still greatly elevated; the corpora quadrigemina run level towards the forehead; the hemispheres are still small; the eyes advance from the sides more forwards; the choroidea resembles a dark ring, broken in its circumference inferiorly and anteriorly (fig. XC. *B*); the nostrils appear as depressions upon the flat face; the branchial fissures are for the most part completely closed, but indications of their presence still continue long after their closure, in the sulci betwixt the former branchial arches (figs. LXXXIX. and XC.). The oral cleft is extensive and gaping; the os coccygis shows itself as a considerable tail bent forwards, and the vertebral incisures are very conspicuous towards the lower part of the vertebral column. The abdomen is closed, with the exception of the umbilical aperture, through which the elongated intestinal loop still passes outwards and inwards, included within the umbilical cord, and in communi-

Fig. LXXXIX.

Fig. LXXXIX.—Embryo, *a* (of five weeks) of the ovum delineated in the preceding figure, contained in its amnion, *b*, which is laid open, with its umbilical vesicle, *c*.

Fig. XC.

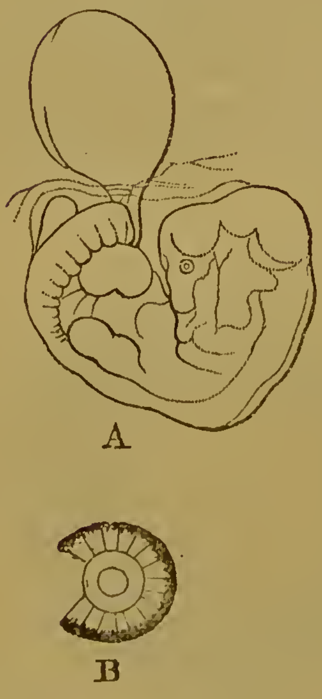


Fig. XC.—*A*, the same embryo as in fig. LXXXVIII. magnified; the brain and spinal marrow are seen shining through the superimposed structures. The corpora quadrigemina are still of large relative size; the nasal fossæ present themselves in front of the eye, in which a vast choroidal cleft is conspicuous. Indications of the second and third branchial clefts are still to be remarked; the umbilical vesicle has a shorter pedicle than in fig. LXXXVI. *B*, is the eye greatly magnified, to show the cleft in the choroid.

cation with the umbilical vesicle, through the medium of its duct, which is continually becoming finer and finer. In the sixth week the embryo is about seven lines in length; its external parts are the same, in general appearance, as in the sixth week (figs. XCI. and XCII.); the forehead, in consequence of the greater development of the hemispheres, is now more vaulted, though the cranium still advances greatly; all traces of the branchial fissures have disappeared, except perhaps a slight cicatrice in the situation of the second posteriorly, and by the boundary of the lower jaw (fig. XC. *i*), and in the situation where the Eustachian tube has been formed. Embryos of this period are easily opened and prepared, and present the various organs in their respective situations, and even with their permanent forms, in the most beautiful manner. (figs. XCI. XCII. and XCIII.). The spinal cord (fig. XC.) is

FIG. XCI.

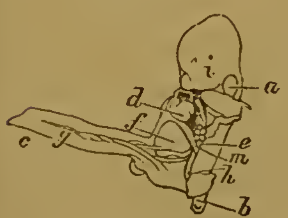


Fig. XCI.—An embryo of the sixth week in outline, of the natural size: *a*, anterior, *b*, posterior extremity; *c*, umbilical cord divided; *d*, heart, with its two distinct atria; *e*, lung of the left side; *f*, left lobe of the liver, at the under edge of which the stomach is situated; *g*, filiform vitello-intestinal duct, entering the protruding loop of intestine; *h*, corpora Wolffiana, and excretory duct of the sexual parts; *i*, sulcus, the remains of the first branchial fissure, which is transformed into the Eustachian tube.

FIG. XCII.

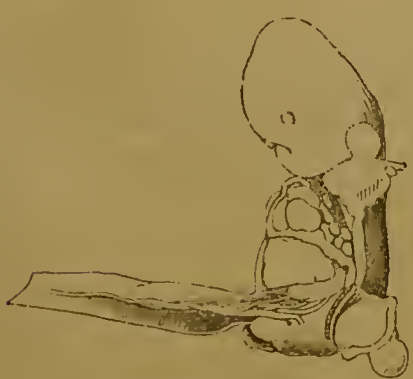


Fig. XCII.—The same embryo depicted of double the size, and with its several parts made out.

FIG. XCIII.

Fig. XCIII.—The abdominal viscera of an embryo magnified four times: *a*, intestinal loop situated in the umbilical cord; *b*, omphalo-mesenteric duct; *c*, omphalo-mesenteric vein; *d*, artery; *e*, stomach; *f*, rudiment of the germinal omentum; *g*, germ-preparing genital organ (testis or ovary); *i*, Wolffian body, with its very delicate excretory duct, which is torn across at *k*, and terminating in the cloaca, *h*; *l*, rudiments of the excretory duct of the germ-preparing sexual organ (vas deferens, or Fallopian tube).

cylindrical, of nearly uniform thickness throughout, and reaches to the coccyx, where it terminates in a blunt extremity; posteriorly, it is open and canalicular. The medulla oblongata makes a bend forwards at the top of the neck, and then ascends perpendicularly into the capacious cranium, where the corpora quadrigemina present themselves as two large semi-globular masses, having behind them a pair of narrow lateral and superiorly yet unconnected laminæ, the rudiments of the cerebellum. The medullary stem, or crus cerebri, passes under the corpora quadrigemina, and again bending downwards, the ganglia of the brain (the optic thalamus and corpus striatum) are evolved upon it in its course, these being covered anteriorly and superiorly by the hemispheres of the brain proper, which in the human embryo acquire a large size at a very early period: these parts, of course, are to be understood as developed in pairs. The first points of ossification appear in the seventh week in the clavicle and lower jaw; the vertebral arches are not yet closed in; the ribs lie on either side of the rudiments of the bodies of the vertebræ as narrow streaks. Rudiments of muscles are not yet distinctly visible, save perhaps in the diaphragm (fig. XCI. *m*), which presents itself, at a very early period, as a thick membranous septum, dividing the thorax and abdomen completely from one another. The heart (fig. XCI. *d*) is already turned leftward; the ventricle is still single, but the septum has begun to be formed; the atria show their separation from the ventricular cavity externally, but internally they still communicate freely (fig. XCIV.); the aorta and pulmonary artery (fig. XCIV. *a*) still arise as a common trunk, which divides into two vascular arches (*b*, *b*), which, however, come together again behind the diaphragm, and there form the aorta descendens (fig. XCV. *h*); the pericardium is complete, and forms a delicate envelope; the lungs lie on either side of the heart, in the angle formed inferiorly between the dia-

Fig. XCIV.

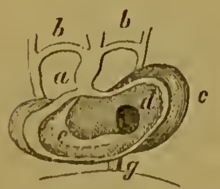


Fig. XCIV.—The heart of an embryo of about the fifth week, laid open upon the abdominal aspect. A very beautiful view is obtained of the manner in which the simple ventricle becomes divided into two separate chambers. The atrium cordis, *c*, still almost quite simple, is pushed backwards; at *d*, the passage from the atrium into the open ventricle is seen; the septum, *e*, resembling a fold of the inner membrane, is perceived rising towards the bulbus aortæ, *a*, which still affords a common origin to the aorta and pulmonary artery; from the bulb arise the two vascular arches, which unite to form the aorta; *g*, vena cava inferior. Figure after Baer, in Siebold's *Journal*, B. xiv.

phragm and the walls of the thorax, and do not yet reeeive any partieular vessels (fig. XCI. *e*) : they are mere saes, not more than about one line in length, but already exhibit traces of division into several rounded vesieles or lobes; they hang by the rudiments of the traehea, a delieate thread, which shows a trifling enlargement superiorly, in the situation of the future larynx. The liver is very large (fig. XCI. *f*), divided into two lobes, and eomposed of small hollow granules, or cœea. Under the left lobe of the liver (*f*), the stomaeh (*e*) is observed of an elongated form, and even now transversely situated; from the part that will become its greater curvature, the omentum majus is seen springing as a very minute appendage or lappet, not above a quarter of a line in breadth; the intestine still shows itself as a long and somewhat twisted loop, extending far into the umbilieal eord (*a*); the duet of the umbilieal vesiele is obliterated, but its remains, in the shape of a fine thread (fig. XCI. *g*, fig. XCIII. *b*) ean still be followed to the umbilical vesiele, now situated at a great distanee from the body of the embryo; the anus is still imperforate. The corpora Wolffiana are now the only organs situated on the vertebral eolumn. It is in the eourse of the seventh week that the kidneys and renal eapsules first make their appearance, and they are speedily followed by the evolution of the germ-preparing sexual organs—the testieles and ovaria, whieh show themselves primarily as small long-shaped bodies. The urinary bladder does not appear before the end of the seeond month; it forms a slight mesial enlargement, which is continued superiorly and anteriorly as a hollow eanal—the uraehus—into the umbilieal eord. In the seventh week the embryo is nine lines in length (fig. XCVI. *l*, fig. XCVII.). The head is of eonsiderable size, and now fairly rounded off; the eorpora quadrigemina, hitherto so largely developed, begin to take the subordinate plaee in point of size which belongs to them in maturity (fig. XCVII.); the eyelids begin to appear, first as perfectly cireular, and by and by as oval folds, over the eye-

Fig. XCV.

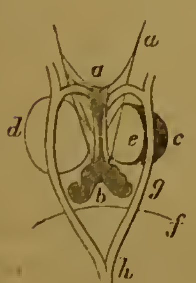


Fig. XCV.—The same heart as in the preceding figure opened from behind. The great atrium, *d*, *e*, is seen, and only the point of the ventricle, at *c*, to the right. The trachea, *a*, *b*, divides and ends inferiorly in the two very small lungs; the aortal arches, *g*, only unite at length in *h*, under the diaphragm *f*, to form the trunk of the aorta; at *a* the nervus vagus is observed.

balls; the anterior breach in the choroid coat is closed; in the ear the concha is formed, with its various eminences and depressions (fig. XCVII. *A*, *e*, and *B*); the mouth is a large triangular space, with one of the angles directed upwards, which still communicates with the future nasal cavity, and occupies nearly the entire breadth

Fig. XCVI.

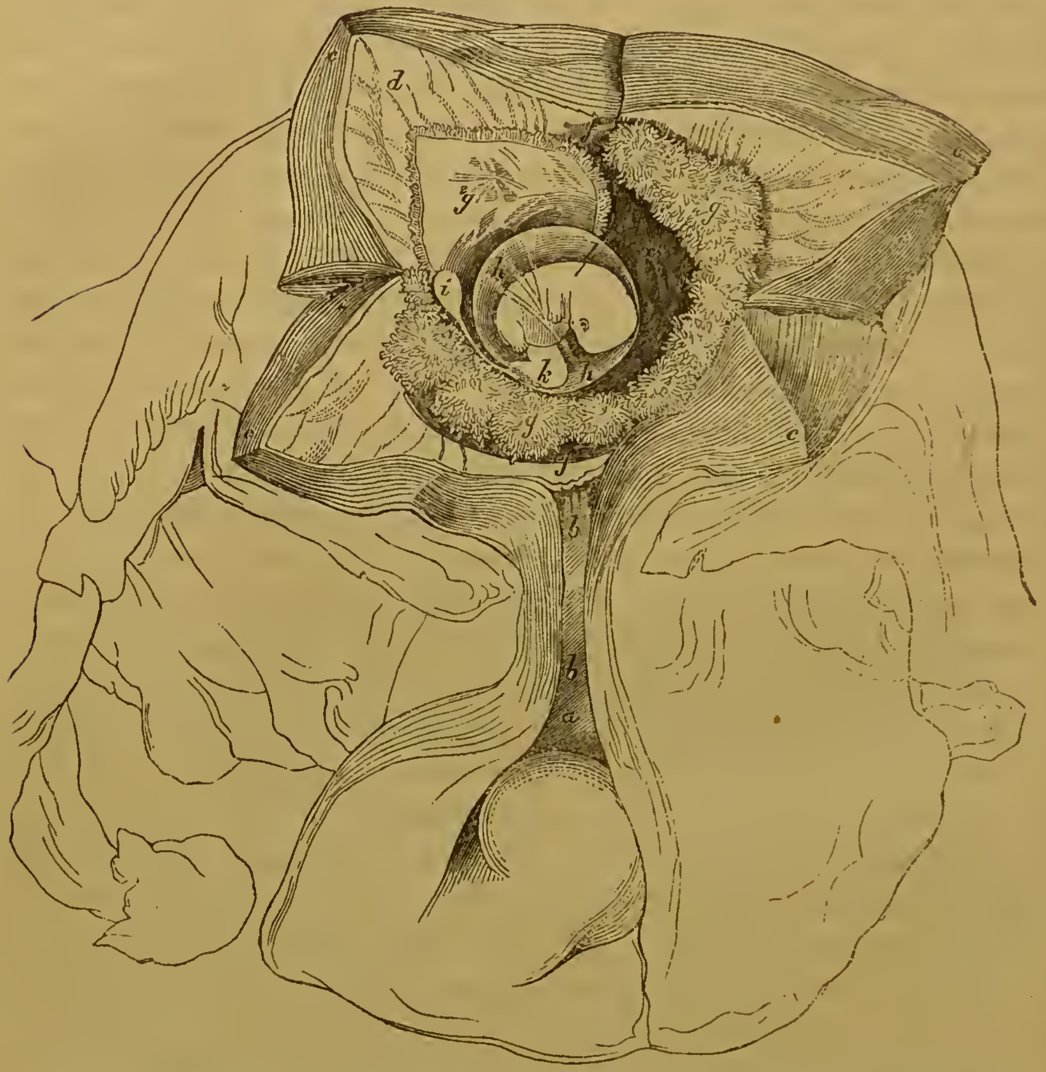


Fig. XCVI.—Uterus, with its contents, in the seventh week of pregnancy: the woman had committed suicide. The embryo, perfectly normal in its conformation, is enclosed in its amnion; betwixt the amnion and chorion the umbilical vesicle is seen; the uterus, lined with the decidua, is laid open, and its parietes are reflected so as to show its contents: *a*, the os externum; *b*, *b*, cervix uteri; *c*, *c*, *c*, *c*, the uterus laid open by a crucial incision, and reflected in four flaps; *d*, *d*, *d*, decidua vera, spread over the uterine surface; *g*, flocculi, or villi of the chorion; g^2, internal aspect of the chorion; *h*, amnion; *i*, umbilical vesicle; *k*, umbilical cord; *l*, embryo; *x*, space for the tunica media, as it is termed, betwixt the amnion and chorion. [The embryo is depicted of its natural size in fig. XCVII. Here the parts are but two thirds the size of nature.]

of the face; the nostrils are two depressions, or pits, with a broad septum interposed between them; the external nose already forms a slight projection (fig. XCVII.). The abdomen appears distended; the parietes of the trunk are still extremely thin. The extremities are more advanced; on the upper extremity the hand, with the rudiments of its five fingers (fig. XCVII. *C*) may be distinguished; the division into arm and forearm is also slightly indicated; the lower extremity is somewhat less forward in its development (fig. XCVII. *D*); still the various divisions of the member can be made out, and even the toes are slightly indicated.

All the particulars just mentioned become still more obvious in embryos of the eighth week (fig. XCVIII. the representation of an embryo, normal in every respect, except an umbilical hernia, *b*, which exhibits many points very beautifully); the head is now relatively larger; the lips begin to be formed; but the tongue, as formerly, lies uncovered in the bottom of the oral cavity; the fingers and toes begin to be distinctly pinched off from the rest of the hands and feet. The embryo is from ten to twelve lines in length, and over a dram in weight; the intestine is now completely retracted into the cavity of the abdomen, and the umbilical cord (cut off at *a*, fig. XCVIII.) is relatively thinner [144].

[144] We have good representations of the embryo during this period; the oldest

Fig. XCVII.

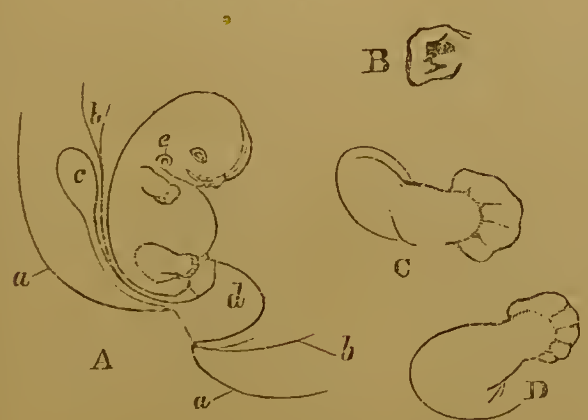


Fig. XCVII. — Embryo from the uterus delineated in the preceding figure: *A*, natural size; *a*, *a*, limits of the chorion; *b*, *b*, limits of the amnion; *c*, umbilical vesicle; *d*, umbilical cord; *e*, external ear. *B*, external ear magnified. *C*, anterior extremity magnified. *D*, posterior extremity magnified.

Fig. XCVIII.

Fig. XCVIII.—Embryo of the eighth week: *a*, umbilical cord cut; *b*, an umbilical hernia; *c*, the ear.

The human Embryo from the beginning of the third month to the period of birth.

§ 74. The particulars that still remain in regard to the development of the human embryo possess a degree of physiological interest much inferior to those we have hitherto related, and their especial consideration belongs to the morphology. It is generally believed that it is in the course of the third month, when the placenta is completely formed, that several considerable and even very important organs first make their appearance; these, however, are most probably present in a rudimentary state during the second month, but are overlooked. The chief of the organs that now become distinctly visible are the thymus, the spleen, the salivary glands, and the pancreas, the muscles, the nerves, the internal parts of the ear, and the ossicula auditus. In the course of the third and fourth months, moreover, we remark a continued progressive formation and transformation of the organs already present in their rudiments, consisting now in a closer approximation to the forms they are to possess permanently after birth, and again in a greater perfection of the forms peculiar to the fœtal state. To the latter head belong the formation of the membrana pupillaris in the third month; the gluing together of the eye-lids first, and then their complete coalescence along their margins, at the beginning of the fourth month; the rapid growth of the capsulæ suprarenales (figs. XCIX. and C. *n*, *n*), which, in the first half of the third month, are as large again as the imperfectly formed kidneys, that consist, at this time, of an aggregation of

by Albinus (*Annot. Academ.* lib. i. tab. i. fig. 12), and then by Soemmerring, Meckel, Burdach, Müller, Kieser, Mayer, &c. I have given new, and, I trust, satisfactory figures of embryos of the fifth, sixth, seventh, and eighth weeks.

Fig. XCIX.

Fig. XCIX.—Embryo of the tenth week, of the natural size, laid open along the abdomen, and the liver and intestine taken away.

three or four little lobules (fig. C. *o*), but which, immediately afterwards begin to diminish, like others of the fœtal organs, particularly the Wolffian bodies, which shrink greatly (fig. C. *s*, *s*) during this period, and finally disappear entirely, although remains of them, especially in the female sex, continue to exist till after birth. In opposition to this decrement of certain organs, the formative energy is aroused to great activity in others, which have remained very much behind in their development; the kidneys, which have hitherto been extremely small, consist, at the end of the third month, of seven or eight lobes, representing the future pyramida Malpighii; the ureters still terminate in common with the external ducts of the sexual organs and Wolffian bodies, and the rectum, in the cloaca or sinus urogenitalis; the rectum is the part which is first detached, and terminates peculiarly in the anus. The most remarkable of the transformations that take place, perhaps, are those connected with the generative organs, for it is at this time that the rudiments of the germ-preparing parts are transformed into testicles or ovaria, and their excretory ducts become vasa deferentia, or Fallopian tubes; that the uterus detaches itself from the upper part of the sinus uro-geni-

Fig. C.

Fig. C.—The same embryo magnified twice; *a*, palatine fissure; *b*, tongue; *c*, carotid of the right side; *d*, *d*, thyroid body; *e*, *e*, thymus gland; *f*, right ventricle, separated by a contraction from the left, *g*; *h*, right, *i*, left atrium cordis; *k*, right lung; *l*, *l*, diaphragm, still very membranous, and to which, at *m*, a small portion of the granular liver still adheres; *n*, *n*, supra-renal capsules (renes succenturiatæ); *q*, *q*, the two laminæ of the mesentery, torn away at the point where these arise from the vertebral column; *o*, *o*, kidneys, composed of lobules, and, at this period, much smaller than the supra-renal bodies; *p*, *p*, ureters; *r*, intestinum rectum cut through; *s*, *s*, excretory ducts and remains of the Wolffian bodies; *t*, *t*, germ-preparing sexual organs, in all probability about to be transformed into ovaries; *u*, sinus urogenitalis, in this embryo, about to become the uterus; *v*, *v*, future Fallopian tubes; *w*, *w*, future round ligaments of the uterus; *x*, clitoris; *y*, longitudinal cleft in the same; *z*, fold behind the orifice of the anus.

talis, and is more fully divided into two cornua; and that the vagina is formed from the lower portion of the same uro-genital sinus; in the male, the urethra is also formed from the uro-genital sinus (vide figs. CI. CII. CIII. and CIV.). The vesiculæ seminales first appear in the fifth month as offsets from the vasa deferentia. The external organs of generation in both sexes have shown themselves so early as the end of the second month, in the

Fig. CI.

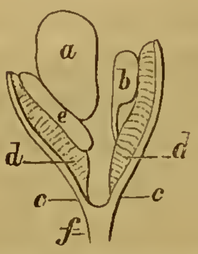


Fig. CI.—Magnified representation of the urinary and genital organs of a human embryo eight lines in length; *a*, supra-renal capsule of the right side, which completely covers the kidney lying behind it; *b*, left kidney, the left supra-renal capsule having been removed; *c*, *c*, excretory portion of the genital organs,—vas deferens, or Fallopian tube; *e*, germ-preparing portion of the sexual system,—testis, or ovary; *f*, sinus uro-genitalis. After Müller (*Bildungsgeschichte der Genitalien*, 1830).

Fig. CII.

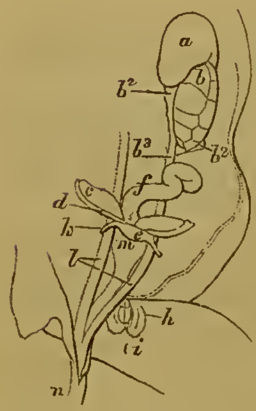


Fig. CII.

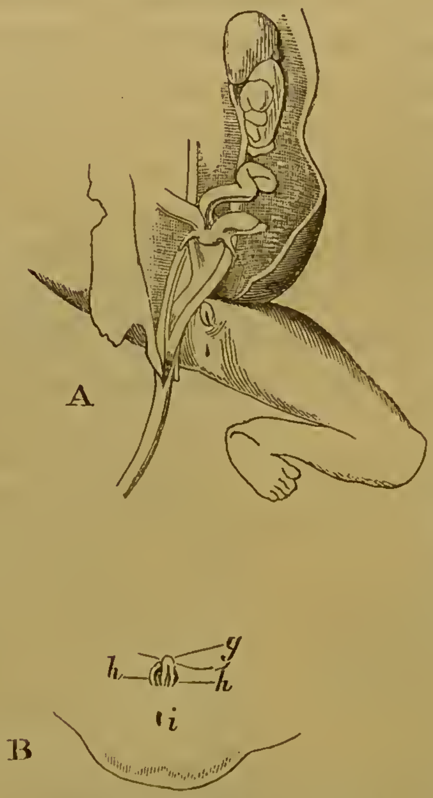


Fig. CII. *A* and *B*.—Internal and external organs of a fœtus of the fourth month, of the natural size. In *A*, the abdomen is laid open; the navel string, *n*, turned down; the left thigh and foot delineated; the club-foot appearance, that appertains to all embryos, is remarkable; *a*, left supra-renal capsule; *b*, kidney composed of many lobules; *b*², *b*², capsule of the kidney removed; *b*³, ureter; *c*; ovary; *d*, Fallopian tube; *e*, uterus; *k*, round ligament, running to the inguinal ring; *f*, rectum; *h*, labia majora, surrounding the clitoris; *i*, anal orifice; *l*, *l*, umbilical arteries; *m*, urinary bladder, produced into the urachus.

B, external genital organs in situ; *g*, clitoris, with the glans and rima, from the bottom of which a fold projects; *h*, *h*, labia pudendi majora; *i*, anus.

The embryo, now figured, bears a strong resemblance to that depicted by Müller (*loc. cit.* tab. iv. fig. 9.) which was 3½ inches long.

shape of small projecting wart-like eminences, which, in the third, acquire larger dimensions, as the clitoris or penis (fig. C. *x*), underneath which, and in the middle line of the perinæum there is a cleft or channel (*g*), which is modified variously according to the sex. In the female, the clitoris continues backward in its formation to the beginning of the fourth month; the lateral parietes of the inferior open channel are formed into the lesser labia, and, in the vicinity of these, the greater labia by and by appear as broader or more extensive tegumentary folds. In the male sex, the inferior open channel of the now erected and prominent penis is closed in the third month, and becomes the urethra, which now terminates on the extremity of the member; the scrotum is still cleft in the middle line, and consists of a couple of folds of common integument. The mouth and nostrils become fairly divided from one another by the formation of the velum palati and dental arches, the wide cleft that lay between them being thus effaced (fig. C. *a*). The dental sacs make their appearance in the lower and upper jaws. The stomach lies more transversely than heretofore; the omenta are more perfectly evolved; the small intestine forms several convolutions, has been entirely included within the abdomen since the tenth week, and now contains meconium; rugæ or folds appear upon the mucous membrane as rudiments of the future villi; the vermiform appendix appears by the side of the cœcum, which has already been some time formed. With the formation

Fig. CIII.

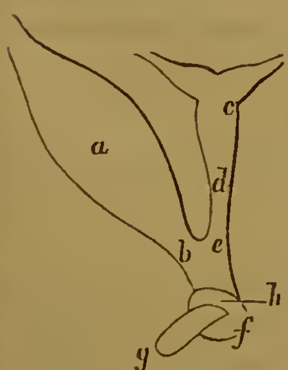


Fig. CIII.—Genital and uropoetic organs of a human fœtus 3½ inches long, from the side; after Müller (*loc. cit.* tab. iv. C.); *a*, urinary bladder; *b*, urethra; *c*, uterus bicornis; *d*, vagina; *e*, anterior still common portion of the urethra and vagina; *f*, common aditus uro-genitalis; *g*, clitoris; *h*, labia pudendi majora.

Fig. CIV.

Fig. CIV.—Internal female genital organs of a human fœtus 4½ inches long to the anus, seen from the dorsal aspect, and magnified; *a*, uterus; *b*, Fallopian tubes; *c*, abdominal end of one of these with its fimbriæ; *d*, ovaria; *e*, remains of the corpora Wolffiana.

of the perinæum in the third month, the anus, which had previously presented itself as a depression immediately behind the common opening of the sinus urogenitalis, appears as a distinct opening (fig. C. *z*), by which the sacrum is hollowed out anteriorly, and made to bend backwards. The gall-bladder, upon the liver, is elongated, and like a piece of intestine. In the heart, the sinuses are large, and divided from one another by external sulci; the division between the ventricles is indicated externally at the apex (fig. C. *f*, *g*,) and the septum ventriculorum is more complete; the Eustachian valve is large. The lungs receive small twigs from the pulmonary artery, which is now distinct from the ascending aorta; but this vessel still divides into two large arches, which by and by unite with two similar arches, proceeding from the aorta. Externally, the division between the head and trunk is more strongly indicated, so that the neck is produced. The abdominal region enlarges, comes forward, and the umbilical cord does not arise so low down, or so near the anus; the umbilical opening is extremely small. The embryo grows, in the course of the third month, to two inches and a half in length, and will weigh an ounce. (fig. CXIII.) The head is particularly large and globular. In the fourth month the embryo increases very rapidly; by the end of this month it measures four inches in length, and weighs about five ounces [142].

§ 75. With the fifth month, the first half of the period of fœtal life is concluded, and the embryo is now about twelve inches long. The epidermic formations now develope themselves particularly: the nails on the toes and fingers, which had already appeared, begin to be consistent or horny; the hair begins to sprout on the head, and the whole body is covered with a soft down—*lanugo*. The first motions of the fœtus are usually experienced about the beginning of the sixth month, and, by the mother, are

[142] Many of the above named organs appear, as I have just said, to be formed earlier than is generally imagined; in the sixth week, for example, I have observed the thymus as two very small, lax, white bodies, situated near and over the heart (fig. XCI.); at the beginning of the third month, this organ is much more distinct (fig. C. *e*); at this time, too, the thyroid gland is visible, and consists of two completely separated bodies (fig. C. *d*, *d*). I have discovered the rudiments of the parotid gland in the seventh week; it then consisted of a filiform excretory duct, upon which, several minute knots or buds, which by and by became sacs, were situated. The spleen appears as a narrow body, on the convex edge of the stomach; and where the stomach is terminating in the intestine, the pancreas shows itself as a congeries of distinct granules. For a more particular account of the development of the sexual organs, vide § 28.

felt as slight flutterings, and then as spasmodic jerks (motion probably oceurs before this, but is not perceived by the parent); a child born prematurely at this time is eapable of breathing. The head is still extremely large, and may, of itself, form a fourth part of the whole body; the faee, from the wrinkles with whieh it is eovered, has the appearanee of that of an aged person; this eharaeter of the physiognomy disappears more and more with the inereased seeretion of fat, by whieh the whole body is rendered rounder and plumper. The resemblance between the external sexual organs, so remarkable on their first appearanee, is entirely lost in the eourse of the preeeding month; but the serotum is still empty; the testicles approaeh the inguinal rings, but only deseend eompletely into the serotum in the course of the eighth or ninth month. At this time also, the glans penis first aequires a complete prepuee, although this part has appeared in the course of the fifth month as a fold of integument. In the seventh month, the embryo or fœtus measures sixteen inehes in length, and weighs about two pounds; it is now eapable of entering on an independent existenee, and, if born prematurely, may be reared. The skin is red, and, besides the fine hair or down, is now covered with a layer of eheesy matter, the *vernix caseosa*,—a substance eomposed of detaehed epithelial nueleated seales and mueus (figs. CV. and CVI.). In the eighth month, the membrana pupillaris disappears; the epidermie sealing of the eyelids begins to loosen. In the ninth month, the bones of the eranium approximate more elosely together, and the fontanelles beeome smaller; the hair, on the head, inereases in quantity, and the woolly hair or down of the

Fig. CV.

Fig. CV.—Epithelial laminæ, three of which are tesselated or connected like a piece of pavement, from the *vernix caseosa* of a new born infant; the cells are depressed, or flat, and transparent; the nuclei spread out; *b*, *b*, are oil-globules.

Fig. CVI.

Fig. CVI.—A single cell of this kind (epithelial lamella), treated with acetic acid, by which the nucleus has become more obvious, and itself exhibits a macula or nucleolus.

body generally falls off; the embryo is eighteen inches in length, and weighs from five to six pounds. In the course of the tenth month, the size and weight of the fœtus vary greatly, measuring from eighteen to twenty inches, and weighing from seven to ten pounds; nor are these by any means the limits, both length and weight being, in some cases, considerably less, and the weight especially, in others somewhat more *.

Birth.

§ 76. The regular period of pregnancy in the human female ends with the tenth lunar month, or the fortieth week. The head of the embryo has now sunk downwards; and the period of delivery being come, it advances first into the os uteri, the membranes of the ovum having previously given way, and is then forced by painful contractions of the uterus through the external organs of generation. In this process it makes a spiral turn in its course, and when the delivery is tardy, and especially when it is irregular from the presentation of the feet, imperfect respiration may take place. In rare cases the child has even been said to have cried before the head was delivered; this is what has been termed vagitus uterinus. The possibility of such an occurrence is not to be denied; its likelihood, however, is very slender, and sources of fallacy or mistake are but too numerous [143].

The Uterus, and the Membranes produced by it.

§ 77. It is familiarly known that those coverings of the fœtus in utero which lie externally to the chorion do not belong to it originally, or are not derived from the ovum, but that they are a product of the new actions set up in the uterus. With regard to the mode in which the membranes derived from the uterus are produced, very opposite views are entertained by different writers. These views have even been elaborated into formal theories, and anatomical facts have been interpreted variously and in support of each by its

[* *Quickening* is the term commonly applied to the first motions of the fœtus as felt by the mother. It usually occurs in the course of the 4th or 5th month. R. W.]

143 The works on midwifery generally speak on the subject of vagitus uterinus; it is also discussed by Burdach, *Physiol.* iii. 95. The cases of vagitus recorded seldom rest on calm and careful observation. Accoucheurs in extensive practice will almost always be found, when closely questioned, to speak of the occurrence rather as something they had heard of, than as aught they had themselves observed. On the mechanism and means of parturition, vide the Third Book of this work.

author. We shall first take cognizance of the relations of these membranes to one another, as they appear on the most careful anatomical examination, and subsequently (§ 82), and altogether independently of the anatomical facts, inquire into the manner in which the ovum may have acquired its uterine envelopes [144]. Researches in regard to the state of the mucous membrane of the uterus, after conception [145], inform us that even before the arrival of the ovum within its cavity an exudation of albuminous fluid takes place from its surface, which, soon acquiring consistency and the appearance of concrete fibrine, is gradually formed into a membrane, thin and delicate at first, but which continually increases in thickness and finally presents a fac-simile or mould of the inner cavity of the uterus. This membrane even appears though the ovum never reaches the cavity of the uterus, but passes through the various stages of its evolution in the ovary, Fallopian tube, or abdomen [146]. In the course of the first week this lining

[144] There is scarcely a subject in anatomy and physiology which has occasioned so much controversy as this doctrine of the decidua. Putting out of the question such researches as are palpably erroneous and insufficient, and false hypothetical interpretations, many of the apparently contradictory opinions may be safely pronounced to be correct in regard to individual cases. The particulars in the text are given from my own reiterated observations and researches, and the views there set forth are illustrated by a series of figures entirely after nature, and by illustrative plans. For an account of the different views that have been held on the subject of the decidua, Burdach, Valentin, Velpeau, Breschet, Seiler, &c. may be consulted, as also my paper in Meckel's *Archiv*, for 1830, on the subject. Among the observers of the past age, Hunter distinguished himself pre-eminently both in profundity of description and in excellence of illustration. He also describes and figures the gelatinous mass which closes the cervix uteri. —Vide his *Anatomy of the Gravid Uterus*, tab. xxv. and xxvii. in the fifth month. I have merely stated facts here, as must be apparent; the explanation of these will be found by and by (§ 82).

[145] The observations of Baer and E. Weber are those that treat of the decidua at the earliest period of its existence, even before the entrance of the ovum into the uterus. Baer has described the decidua and its vascular connexions a week after conception.—Vide Siebold's *Journal*, vol. xiv. p. 403, with a figure, which is copied in fig. CVII. Weber's account of the decidua occurs in his edition of *Hildebrandt*, vol. iv. p. 466.

[146] The decidua is certainly found in the greater number of extra-uterine conceptions; when it is not found, it is perhaps overlooked, or mistaken for the spongy mucous membrane of the uterus. I have found it in this state in the uterus three or four weeks after parturition; [or the converse of this may be true; that which has been described as decidua vera in cases of extra-uterine gestation may have been but the mucous membrane of the uterus softer and more spongy than usual; or, otherwise, the uterus may have been lined with a plastic deposit preparatory to the reception of the ovum; but

fills all the foveoli or depressions of the mucous membrane of the uterus, and blood-vessels shoot from the uterus into its substance, so that it becomes organized; formal capillary retes may be demonstrated surrounding the villi of this new formation which penetrate the little depressions of the proper mucous surface (fig. CVII.). The thicker the membrane grows, the more perfectly does it become organized; its inner aspect, or that turned towards the cavity of the uterus, is smooth; its outer aspect, by which it adheres to the uterus, is villous and rough. Its thickness in the third or fourth month of pregnancy, when it is most perfectly developed, may be about a line, and at this period it may be completely detached from the uterus and exhibited apart (fig. CVIII.),

this may have been, nay, from the accounts often given of it and its appearance in preparations, certainly was different from the proper decidua, being a soft, lardy-looking, very thick, and unorganized layer,—not a thin reticulate vascular tissue, like the true decidua. That the decidua vera is no absolute product of the uterus, but of those living tissues with which the living ovum is in contact, seems demonstrated by this : that the ovum in extra-uterine gestations of all kinds is surrounded by a membrana decidua as it is when lodged in the cavity of the womb. When the ovum makes its way in due season and unimpeded into the uterus, it acquires its decidual covering there; if it be detained in the tube there it acquires its decidual covering likewise, and the uterus is without this membrane. The uterus having been found in a single instance of ovarian or tubal conception without the decidua, seems to the writer fatal to the theory of that membrane being the product of the uterus independently of the presence of the ovum. Nature admits of no exceptions to her laws. The decidua, indeed, as the bond between the mother and the embryonic chorion, is a formation indispensable to the development of the germ wherever this happens to take place, whether within the uterus, in the Fallopian tube, or in the cavity of the abdomen. There are two preparations of tubal gestation in the Museum of St. George's Hospital, which, whatever may be said as to the presence or absence of the true decidua in the uterus, certainly demonstrate the existence of this membrane around the ovum arrested in the Fallopian tube. See also a note by Dr. R. Lee, on the situation of the decidua in cases of extra-uterine gestation, in the *Lond. Med. Gazette,* for June, 1840. R. W.]

Fig. CVII.

Fig. CVII.—Internal superficies of the uterus with the decidua of Hunter in process of formation, from the body of the female from which the drawing of the Graafian follicle, given in fig. LIX was made. The villi, *a, a, a,* of the mucous membrane of the uterus have increased notably in length. The matter which is to become the membrana decidua is observed deposited between and upon the surface of the villi; *c, c,* are the uterine vessels extending into the decidua and there forming loops. (After Baer, *loc. it.*)

it is then of a reddish gray, or whitish gray colour, and presents the consistency of concrete fibrine; examined under the microscope, it is found to be entirely composed of flattened cells, which have nuclei of from the $\frac{1}{200}$th to the $\frac{1}{300}$th of a line in diameter, and in addition to these, dark kernels more or less replete with fine molecules (as fluid of the cells)—(fig. CIX.); the cells are tessellated or arranged like a piece of pavement, one by the side of and laid over another, and are altogether different from the

Fig. CVIII.

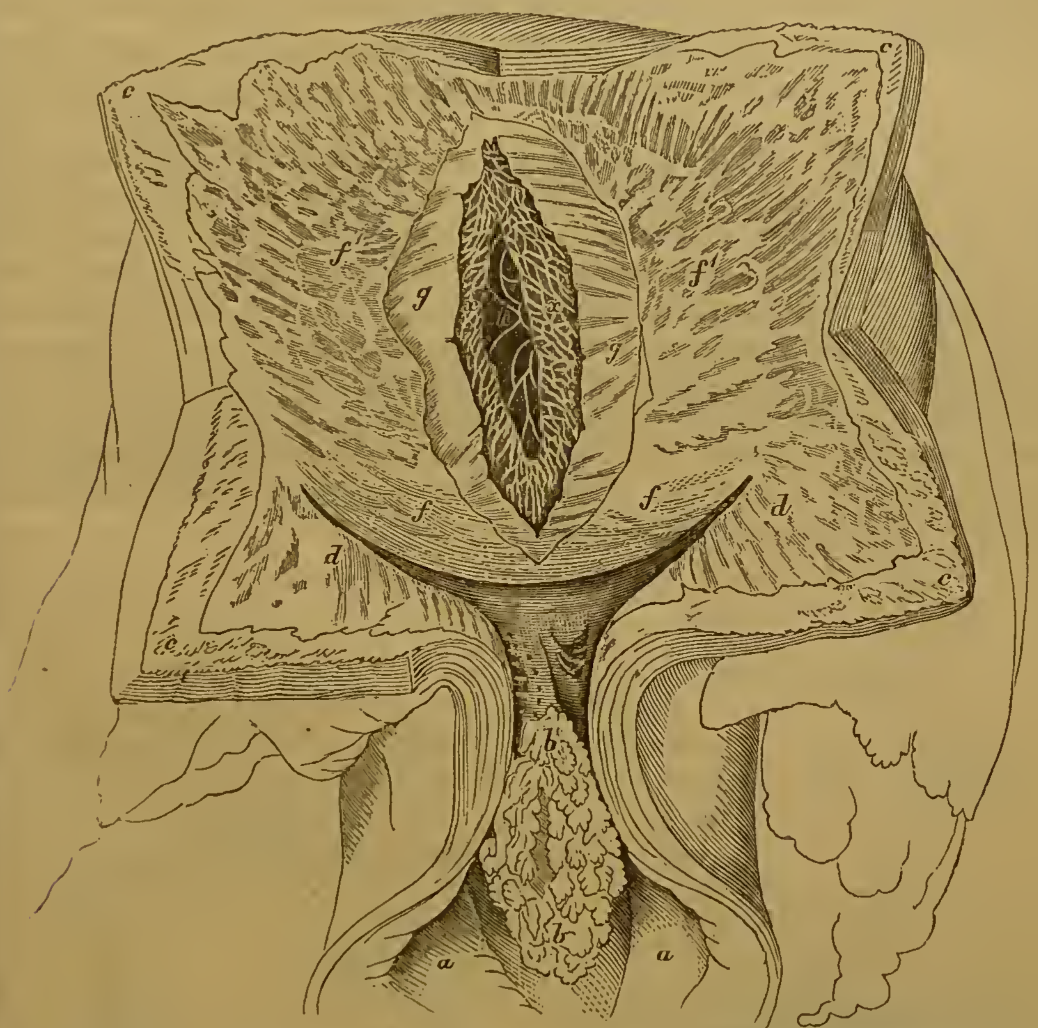


Fig. CVIII.—The gravid uterus at the end of the fourth month laid open and the involucra of the ovum delineated in situ. In the cervix uteri there is a great plug of gelatinous matter, the villi of which, from the preparation having been immersed in alcohol, are extremely distinct.—*a*, Os externum; *b*, *b*, gelatinous plug filling the cervix uteri; *c*, *c*, *c*, the uterus reflected in four flaps; *d*, *d*, decidua vera lining the uterus; *f*, *f*, the decidua reflexa passing into the vera by a circular fold, still smooth and unconnected inferiorly; at f^1, f^1, however, it is rough, as at this part it was in contact with the decidua vera, and was only separated from this by force; *g*, villi of the chorion; *h*, amnion; *x*, *x*, *x*, *x*, tunica media, lying betwixt the amnion, *h*, and the chorion, *f*, and forming a veritable membrane.

cylinder-epithelium of the proper uterine mucous membrane, which at this time appears to have been detached, and given way to a new production. The DECIDUA VERA, as this new membrane is called, either forms a completely shut sac, in which ease it covers the orifices of the tubes, and even sends processes into them and the os uteri; or it forms a pouch partially shut, being wanting in these situations; the decidua is most commonly absent over the os uteri, where considerable flap-like appendages or growths occasionally present themselves hanging from it (plan, fig. CX. and fig. CXIII.); it is also frequently wanting over the mouths of the Fallopian tubes (fig. XCVI.)[147]. It is only now and then that the decidua vera is formed extending some little way into the

[147] I am firmly persuaded from my own experience that the hotly contested point of the presence or absence of the three openings amounts to nothing. Every one, from the time of Hunter, who has described one, two, or three openings, or who has denied the existence of any, may in his turn be right, or he may be wrong: if the exudation have been copious, the whole of the three natural openings of the uterus may be covered, and a completely closed membrane thus produced; but the exudation being more scanty, one or two, or all three of the openings may escape a covering, and then there is a decidua with a corresponding number of outlets; the opening into the cervix uteri as the largest of the three openings is most apt to escape a covering, and so it is here that the decidua is most frequently found defective.

FIG. CIX.

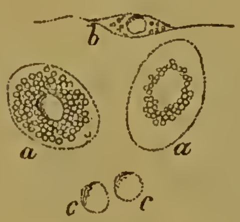


Fig. CIX.—*a, a,* Cells of the decidua vera of a recent ovum of six weeks; the nucleus in the middle is surrounded by molecules; *b,* section of a cell of this kind; *c, c,* nuclei removed from the cells, of the $\frac{1}{200}$th and $\frac{1}{300}$th of a line in diameter.

FIG. CX.

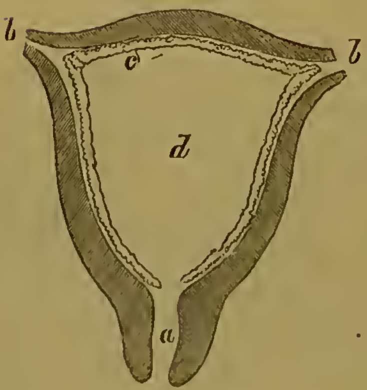


Fig. CX.—Sectional plan of the uterus about eight days after impregnation; *a,* neck of the uterus; *b, b,* entrances to the Fallopian tubes; *c,* decidua vera, covering the walls of the uterus at every point; *d,* cavity of the uterus.

cervix uteri, within which a plug of gelatinous-looking matter is generally observed, that acquires great consistency by digestion in alcohol, looks villous on the surface when detached, and is produced from the foveoli of the mucous membrane of the part it occupies. This gelatinous production appears as a delicate exudation in the second month, acquires size and consistency in the third (fig. CXIII.), and reaches its highest development in the fourth (fig. CVIII.); it may be regarded as a peculiar formation, and attains its most perfect state at the same time as the decidua vera. If the uterus be examined during the first half of the period of pregnancy,—and researches are best made in the course of the second and third month,—the ovum will be found not to be surrounded immediately by and in contact with the internal surface of the decidua vera, but to be included within a pouch of this membrane, which consequently looks as if it had grown inwards at a particular place and hung like a sac containing the ovum into its own internal cavity (plan figs. CXI. and CXII. and figs. CVIII. and CXIII.). The membrane which surrounds or covers the ovum immediately is called the *decidua reflexa;* in structure it is precisely similar to the decidua vera, but on the whole thinner, smooth on its outer surface, which is turned towards the decidua vera, and, like the inner aspect of the latter, furnished with slight depressions; towards the ovum, again, it is rough or shaggy, and its processes, or villi, hang towards and coalesce with those of the outer aspect of the chorion, from

Fig. CXI.

Fig. CXI.—Plan of the uterus at the moment when the ovum *f*, surrounded with its chorion *g*, is entering its cavity, and pushing the decidua vera before it to form the decidua reflexa. *a*, Neck of the uterus; *b*, *b*, entrances to the Fallopian tubes; *c*, decidua vera, covering the walls of the uterus at every point; *d*, cavity of the uterus.

which, though they may be easily enough separated at first, this is done with more difficulty by-and-by, and in the third month it is not to be accomplished at all. At one part the ovum is covered neither by the decidua vera nor by the decidua reflexa; this is where the placenta is formed, and usually indicates the point of reflexion of the decidua reflexa; here there is a thick stratum of a substance precisely similar to the decidua reflexa, which attaches the ovum to the wall of the uterus, and which blends intimately on the outer side of the reflex fold with the decidua vera; this thick stratum is named the *decidua serotina,* from its appearing to have been formed at a later period. In those cases in which extra-uterine conception has taken place, the decidua vera alone is met with, the reflexa and serotina are wanting. The cavity then contains an albuminous fluid, which, in ordinary cases, also occupies the space between the decidua vera and decidua reflexa, so long as the two continue unconnected (*hydroperione* of Breschet).

These twofold membranes, the decidua vera and decidua reflexa,

Fig. CXII.

Fig. CXII.—Sectional plan of the uterus with the ovum further advanced; the cervix uteri is now plugged up with a gelatinous mass, *a*; the decidua vera, *c*, sends a process, c^2, into the right Fallopian tube; the cavity of the uterus is almost completely occupied by the ovum; *e, e,* points of reflexion of the decidua reflexa; *f,* decidua serotina; *g,* allantois; *h,* umbilical vesicle, with its pedicle in the umbilical cord; *i,* amnion; *k,* chorion; between the two the space for the albumen.

may be not unfrequently demonstrated in aborted ova of the first three months; occasionally the ovum is surrounded by both the sacs shut and quite entire; more commonly, however, the decidua vera can alone be traced, and that is in flaps of various sizes (fig.

Fig. CXIII.

Fig. CXIII.—Uterus, with an included ovum, in the twelfth or thirteenth week of pregnancy. The cervix uteri is closed with a mucous or gelatinous plug; the membranes are opened and the embryo is taken *e situ*, but is still attached by the naval string. *a*, Os externum; *b*, *b*, gelatinous plug of the cervix uteri; *c*, *c*, *c*, *c*, the uterus reflected in four flaps; *d*, *d*, *d*, *d*, decidua vera spread over the inner aspect of the uterus; *e*, *e*, two great smooth flaps of the decidua vera, drawn somewhat apart; they closed the internal orifice of the uterus; *f*, *f*, decidua reflexa, passing by a circular fold or reflexion into the decidua vera; *g*, *g*, *g*, villi of the chorion; *h*, amnion; *i*, umbilical vesicle; *k*, umbilical cord; *l*, embryo; *m*, opening of the decidua into the orifice of the left Fallopian tube; *x*, space between the amnion and chorion for the tunica media. [The parts are represented of two-thirds the natural size.]

LXXXVIII. *a, p*), hanging from the point of reflexion. The decidua reflexa is usually much altered, and thicker instead of thinner than natural, in consequence of the infiltration of blood into its substance,—an accident which is often intimately connected with the occurrence of abortion [148]. In some few instances the reflexa seems actually to be wanting, a fact for which researches on the pregnant uterus itself, as well as on otherwise normal aborted ova, appear to vouch [149]. In the later periods of pregnancy, the two deciduous membranes are parted with increasing difficulty, and at last they are not to be separated at all; they grow together probably in consequence of the contact and the pressure occasioned by the enlarged and still enlarging ovum; but even in ova that have attained maturity, and in the after-birth, they can still be demonstrated as a simple, pretty thick, and cohering membrane [150]. Still later, for several weeks after parturition, the mucous membrane of the uterus is extremely loose and spongy, and small shreds or portions of it are even thrown off along with the lochial discharge.

148 Such cases, in which in aborted ova the decidua vera presents itself in a varying state of completeness over the reflexa, are very numerous, and I should say that a flap at the point of reflexion was the rule. As observations upon this point are far more readily made on aborted ova than on such as are still contained in the uterus, I shall here mention a few particular places where they may be consulted, merely stating that fig. XC. may be taken as a kind of type of them all:—Hunter, on the *Gravid Uterus*, tab. xxxiii. figs. 1, 2, 3, 4, copied by Loder, *Tab. Anatom.* tab. xc. figs. 1, 2, 3, 4; Velpeau, tab. viii. figs. 3 and 7, tab. xi. fig. 2; Breschet, tab. ii. fig. 3, tab. iv. fig. 5; Bock, *Diss. de Membrana Decidua Hunteri*, Bonn, 1831; Kilian, *Geburtsh. Atlas*, tab. xxiv. fig. 2, where the figures are as true to nature as they are beautiful; Mayer, *Icones Selectæ*, Bonn, 1831, tab. v. fig. 7.

149 I have never found the decidua reflexa wanting in the uterus, although this is said occasionally to be the case by several observers. But then it was wanting in the normally-formed ovum of the third week, represented in fig. LXXXIII.; here the decidua vera surrounded the ovum closely with its smooth surface: it was shaggy externally, completely closed, and formed a mould of the inner cavity of the uterus; it was readily detached as a complete sac. On the possibility of the occurrence of such a formation of the decidua, vide later (§ 82).

150 Hunter was aware of the persistence of the decidua to the period of birth, and speaks of the mode in which it presents itself in the secundines; but Bischoff, in his "*Contributions to the Doctrine of the Membranes of the Human Fœtus*" (*Beiträge zur Lehre von den Eihüllen*, &c. Bonn, 1834), gives a more particular account of the matter. He shows the presence of two membranes in the after-birth, which are unquestionably the united decidua vera and decidua reflexa. What Bischoff speaks of as probable, I have had occasion to confirm in regard to both the vera and reflexa being originally furnished with vessels; they are only fewer in the latter than in the former. The cells are still very dis-

Among the mammalia a decidua vera can always be demonstrated, but in none of them does the decidua reflexa appear to be present [151].

Of the Fœtal Envelopes produced originally from the Ovum, or subsequently from the Embryo.

§ 78. At the earliest periods at which human ova have yet been examined in the uterus,—and this has been when they were but of the size of a pea,—the CHORION has been found surrounding the embryo loosely as a simple membrane, shut on all sides, smooth internally, rough from the presence of short cylindrical villi externally,—a kind of epithelial basis of the future membrane, with its various peculiarities [152]. In ova that are somewhat farther advanced,

tinct here, and look like transparent bladders, often full of molecules, but with very clear nuclei.—Vide fig. CXIV.

[151] In the bitch, precisely as in the human subject, there is a lining membrane analogous to the decidua in all respects, formed in the uterus before the arrival of the ova within its cavity ; it is vascular, thick, and covered on its surface with large cells like those of a honeycomb.—Vide Baer, in *Entwickelungsg.* ii. 242, and Bojanus's *Figures in Nova Acta Acad. Nat. Cur.* vol. x. pl. viii. fig. 1, b. ii. 3 c. The reason of the absence of the decidua reflexa in animals as well as of its presence in man, lies in the dissimilar form of the uterus and relations of the oviducts to it; in animals, the oviduct or Fallopian tube expands and opens gradually, or rather is continued freely, into the uterus; in the human subject, on the contrary, it enters the thick walls of the uterus as a very slender canal, and opens by a narrow orifice and at a right angle upon its inner surface.

[152] It would be needless here to mention the numerous writers on the chorion and the rest of the fœtal membranes; I shall merely quote particularly the monograph of Bischoff upon the subject, entitled, "Contributions to the Doctrine of the Membranes of the human Fœtus" (*Beiträge zur Lehre, &c.*, Bonn, 1834.), written with much critical acumen, and based on numerous individual inquiries. The account in the text is principally after my own observations and inquiries. Some microscopical researches upon the membranes by Breschet and Gluge will be found in the *Ann. des Sciences, Nat.* t. viii. p. 224, with which my

FIG. CXIV.

Fig. CXIV.—Cells of the placentary decidua of an ovum arrived at the full time. The nuclei are extremely plain; in the cells *b*, *b*, treated with acetic acid, the granular corpuscules of the nuclei have become apparent.

the villi are less crowded; they protrude in the form of considerably broader vesicles; the spaces betwixt them are wider and smooth, and they end in more delicate, rounded extremities. At the beginning of the second, perhaps in the course of the first month, the villi are observed to divide into branches, which arise from short thin stems, and terminate either thin or filiform, or in vesicular enlargements (fig. CXV.). The smooth interspaces increase continually in extent; the membrane even shows a general tendency to become naked, all but in one particular part, which was without villi at an earlier period; this now becomes thickly covered with villi, and here they go on increasing in a much greater proportion than in other situations, so that the chorion of ova about the middle of the period of pregnancy is generally smooth externally, whilst in the part indicated, the dendritic villi are large, closely crowded together, and here coalesce in an especial manner with the decidua, pushing their ramifications into the thick stratum of the decidua serotina: in this manner and in the course of the third month is the PLACENTA formed. The chorion is entirely without vascularity, and is a membrane made up of cells, which in many parts compose a structure that bears the closest resemblance to that of vegetables; each cell contains a large distinct nucleus (fig. CXVI.); the villi participate in the same structure, but their cells are farther filled with a granular matter. (fig. CXVI). From the inner wall of the chorion, especially over the placenta, a layer may be detached

own observations agree in the main. Perhaps the best drawings of the chorion, and its appendages, extant, occur in Seiler's work, "The Uterus and Ovum of Man (*Die Gebärmutter und das Ei des Menschen*, Dresden, 1832).

FIG. CXV.

Fig. CXV. One of the villi of the chorion arising by a single root, but dividing into numerous branches, natural size. It is one of the villi of the ovum depicted in Fig. XCVI.

FIG. CXVI.

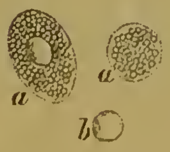


Fig. CXVI. Cells from the villi of the chorion of a recent ovum of the sixth week: *a, a,* cells plentifully filled with molecules; *b,* a nucleus isolated.

more or less obviously, which is very vascular, penetrates among the villi, and carries in large convoluted bundles of vessels, which run to the ends of the villi. This vascular lamina, which cannot be demonstrated at every point of the circumference, is named the ENDOCHORION, in contradistinction to the outer lamina, which is called the EXOCHORION[154]. In ova that have not been injured, and in such as are examined in situ within the uterus during the third and fourth months, a separate, extremely delicate arachnoid membrane will be observed enveloping the amnion loosely, but completely, and situated between that membrane and the chorion (fig. CVIII.). This membrane may also be readily demonstrated in its separate condition through the whole of the second half of the period of pregnancy, and even in the secundines of ova that have attained the full period. It is usually distinguished by the name of the *tunica media*, or middle tunic[155]. In the first months of pregnancy, instead of the membrane now described, an albuminous mass of very various consistency is found, often intermingled with numerous flocculi and threads, occasionally pulpy or gelatinous, and still oftener arachnoidal in its characters. Put into spirit, this mass assumes the appearance of the cellular tissue that is found between the muscles, and seems in fact to stand in the same relation to the amnion and chorion as the intermuscular cellular membrane does to the fasciculi between which it lies: this mass occupies the space, in young ova still considerable, which intervenes between the amnion and chorion (fig. XC. *f*). This matter or tissue has been designated by different names, and been very commonly compared to the albumen of the egg of the bird and certain other animals[156]. Next comes the amnion, which envelopes the fœtus immediately, lying very close to it in the earlier periods, and being continued immediately into the outer covering or common integument of the embryo by the open abdominal parietes (fig. LXXXVIII. and figs. CXXIII. and CXXIV.). In older ova the amnion is in contact with the chorion, or rather with the inter-

[154] The distinction between the exochorion and endochorion was drawn by Burdach; the latter he regards as formed by the union of the allantois. Vide § 80.

[155] Bischoff has given a careful account of the tunica media as a distinct membrane in ova at the full time (l. c.); I have again and again observed it in ova of every age; I agree in essentials with Bischoff's view, that it is formed by the compression and consolidation of the mass named the albumen ovi.

[156] This formation, described by Müller, Valentin, and others, as albumen, is spoken of by some (Velpeau for instance) as the allantois, and is called by different names—arachnoidal membrane, magma reticulare, &c.

posed tunica media; but from this it is easily removed: it covers the umbilical cord externally, and at the umbilicus is continuous with the common integument of the fœtus: it is filled with a watery, very slightly albuminous fluid, the liquor amnii, in which flocculi (epithelial scales detached from the surface of the embryo) are commonly seen suspended. The liquor amnii shows strong alkaline reaction, and contains albumen and salts of the phosphoric, sulphuric, and carbonic acids [157].

Of the umbilical Vesicle.

§ 79. The difference and dispute to which the umbilical vesicle gave rise among the writers of the by-gone age, may be held as reconciled and ended by the concurring views of observers of the present day [158]. It is now satisfactorily demonstrated, that the umbilical vesicle is constantly present as a normal formation in the earlier months of pregnancy, and that it is connected with the intestinal canal. Repeated observation has shown that the umbilical vesicle is relatively very large in the youngest embryos, that it rests immediately upon the intestine, and communicates with its cavity, having, at this time, a rounded or oval form (figs. LXXXIV. and LXXXV.). At a very early period, however, it becomes pedunculated; its neck is produced into a canal, which is hollow at first, so that its contents can be pressed backwards and forwards into the bowel [159]. This canal or pedicle is of very different

[157] Writers seem to agree much more generally in their views of the amnion than of any of the other membranes; few, however, have seen it still open, and enveloping the embryo closely. Vide § 72. According to chemical analysis the liquor amnii contains from ninety-six to ninety-eight parts of water, from one to three parts of albumen, and smaller quantities of the lactates and phosphates of soda, and a little potash. The statement of Frommherz and Gugert that the liquor amnii contained urea, Berzelius regards as requiring confirmation; physiologically such a circumstance is very unlikely.

[158] Mayer seems the only modern anatomist who still seems to call in question the original communication of the umbilical vesicle with the intestinal canal, although he admits its analogy with the vitellary sac of birds. (*Nov. Act. Acad. Nat. Curios.* vol. xvii. p. 555.)

[159] Velpeau, in the plainest manner, saw that the pedicle was hollow, in different ova he could press the yellowish fluid contained in the vesicle into the intestine (l. c. p. 33). Baer says (l. c. p. 271), "that this yolk-duct is a pervious canal, I have satisfied myself, I think in almost every ovum of six weeks that I have yet examined; in some, I found the communication very free, and once I distinctly saw vitellary matter in the lower intestine." These views, themselves deduced from observation, are supported by the researches of Hunter, Pockels, Bojanus, Oken, Kieser, Müller, Burdach, Bischoff, and myself. The umbilical

lengths in different embryos; in those that are more mature, the umbilical vesicle is often found nearer the abdomen than in others that are much less advanced. It does not long remain pervious; at the end of the first month it is already filiform (fig. LXXXVI.). With the increase of the amnion, the umbilical vesicle is found as a pyriform body betwixt this membrane and the chorion (fig. XCVI.); it collapses more and more; the pedicle is obliterated in the second month, and becomes an extremely fine thread, which, however, may be traced to the end of the noose of intestine contained within the umbilical cord (figs. XCI. *g*, XCIII. *b*). Such continues to be the condition of the umbilical vesicle to the end of pregnancy, when it may still be demonstrated in the membranes; the shrunk vesicle itself may be discovered between the amnion and chorion, and a filiform appendage traced from it into the umbilical cord [160]. It contains a yellowish white, sometimes yolk-yellow coloured fluid, in which numerous globules and oil-globules are suspended. It appears to consist of two laminæ, an external vascular, and an internal mucous layer, which, as in the yolk-bag of birds, generally presents a villous and plicated inner superficies. It rarely happens, that anything like a vascular rete can be perceived externally; when it is apparent, its meshes are rhomboidal in figure, and cover the entire surface (fig. CXVII.); it is much more common to observe blood-vessels on the pedicle; these consist of an artery—the omphalo-mesenteric artery, which arises from the aorta, and passes over the intestinal loop of the

vesicle, however, it is well to be aware, is very commonly found obliterated in aborted ova of six weeks: vid. figs. XCI. XCII. and XCIII. One of the best figures of this relation of the umbilical vesicle to the intestine extant is that of Kieser, which is contained in his work, *On the Origin of the intestinal Canal, from the umbilical Vesicle, (Ueber den Ursprung des Darmkanals, &c.* Gotting. 1810.)

[160] This late existence of the umbilical vesicle has recently been particularly demonstrated by Mayer (l. c.) and illustrated by very beautiful drawings.

Fig CXVII.

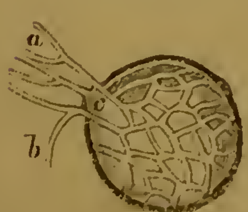


Fig. CXVII.—A magnified umbilical vesicle, somewhat freed from super-imposed structures, to show the vascular net-work that covers its surface; *a* and *b*, portions of the amnion; vessels are seen proceeding from these points towards the umbilical vesicle; *c*, duct of the umbilical vesicle, returning to join the intestine. (After Baer, loc. cit.)

umbilicus (fig. XCIII. *c*), and a vein—the omphalo-mesenteric vein, which terminates in the vena cava *d* [161].

Review of the doctrine of the Allantois.

§ 80. No part, in the history of the development of the human embryo is so obscure, or none so difficult to study, as that which has the ALLANTOIS for its object; no where is it more necessary to revert to the development of birds and mammalia to seek light than here. In the chick we have seen the allantois formed from the lower intestine, and making its appearance on the third day as a pyriform vesicle, which grew rapidly, consisting originally of the mucous layer above, but receiving a covering from the vascular layer at a very early period, and then presenting a thick net-work of blood-vessels, consisting of two umbilical arteries, and an umbilical vein. Thus constituted, the allantois shoots into the space between the amnion and the serous investment, grows quickly around the embryo as a flattened bag or bladder, lying all the while close to the membrane of the shell, and coalescing by its two contingent surfaces, it finally forms a membrane that envelopes the ovum or embryo completely, and is now known by the name of chorion. The allantois of birds continues in open communication with the cloaca by means of a pedicle, and the fluids secreted, in the first instance by the Wolffian bodies, and then by the kidneys, are transmitted to its cavity, which, therefore, actually contains urine, and often, by the end of the period of incubation, whitish concretions or deposits, which, when examined chemically, are found to consist in great part of uric acid [162]. In all the orders of mammalia, so far as observation has yet extended, an allantois has been found to be formed in a very similar manner; it arises as a small vesicle from the cloaca, and is speedily covered by a vascular lamina, carrying along with it, precisely as in birds, two umbilical

[161] Kieser has given figures of these vessels, and they are finely shown in the figure of an ovum of eight weeks, by Seiler (*op. cit.* tab. x.). Baer has likewise represented the vascular rete of the umbilical vesicle in an ovum of the fifth week; he could discover no sinus terminalis; on the inner surface of the umbilical vesicle, however, he discovered extremely minute villi, similar to those of the yolk-bag of birds (*op. cit.* ii. tab. vii. figs. 18, 19).—Siebold's *Journal*, p. 406, fig. v., copied fig. cxvii. Vide also corresponding relations of the vessels in the dog, fig. LXXIX. *A, B, C,* p. 159, after Bojanus.

[162] On the development of the allantois of birds, vide the first chapter of this section. Jacobson found the whitish concretions composed almost entirely of uric acid.

arteries from the aorta, and two veins, which generally unite into a single trunk, and proceed as the umbilical vein to the vena cava. With the formation of the navel-string, the portion which lies within the abdomen becomes partially divided at the umbilicus from that which lies without it; the intra-abdominal portion enlarges, and is transformed into the urinary bladder; the constricted portion at the umbilicus lengthens out into a hollow canal—the urachus, which leads to the extra-abdominal portion or allantois, which now presents itself as a bladder of various size and figure, lying between the amnion and chorion, and filled with fluid, which, as in birds, is at last urinous in its characters. In many families of mammalia, as, for example, in the solidungula, where the allantois grows to a great length, tears through the chorion at either end, and distends the whole uterus, the vascular is detached from the mucous layer; the former shoots with its vessels into the chorion; the latter remains as a completely unvascular sac, in communication with the urachus. In the carnivora, the allantois arises in the same manner, advances, coalesces by its outer most vascular surface with the chorion, sends processes into the villi of this membrane, and thus forms the placenta; here there appears to be no separation of a mucous layer (fig. LXXIX. *A*, from the dog)[163]. White concretions are also frequently found in the fluid of the allantois of many mammalia. In the human being it is only in the very earliest periods that traces of an allantois can be discovered; but the observations that bear upon this point are helped out, and rendered more complete by the occurrence of certain abnormal states, occasionally met with in ova of an early period, in consequence of imperfect development, or an arrest of evolution experienced in some prior stage. In embryos from a fortnight to three weeks old, in which the abdomen is still widely open, a pyriform bladder is seen springing from the lower extremity of the intestine, which contains vessels, and is directed towards the chorion; embryos often perish before this has occurred, when the allantois lies in the form of a bladder, near or under the umbilical vesicle[164]. In ova that are somewhat

[163] Baer describes the various forms of the allantois in particular families of mammalia in the second part of his *History of Development*, p. 193.

[164] I am disposed to regard the representation of Poekels (*Isis*, 1825, tab. xii.) of Coste (*Embryologie*, tab. iii. figs. 4 and 5,) and of Baer, (in *Siebold's Journal*, figs. vii. and viii., and *History of Development*, tab. vi. figs. 16 and 17,) as instances in which the human allantois is more or less obvious, in some of which indeed it has retained its genuine original form.

farther advanced, this bladder is observed to have become broader, and is in contact to a greater or less extent with the chorion (fig. LXXXV. h—n); here it is easy to trace the broad open duct from the cloaca to the chorion (n^1); about this time the mucous layer seems to separate from the vascular layer; the latter, in all probability, betakes itself, in its rudimentary state, to join the chorion; with the closure of the abdomen, and the greater extent to which the mucous layer is produced, the duct becomes continually smaller and narrower; though it may often still be inflated with air in the course of the fifth week; the funnel-shaped extremity with which it approaches the chorion is perceived, and here, white concretions, like little pieces of friable chalk, are frequently met with [165]. Towards the embryo, again, the duct becomes wider, and terminates in the urinary bladder, which has just been separated from the intestine. Small pear-shaped vesicular dilatations often remain within the navel-string, which are more or less distinct from the tract of the duct, and are frequently occasioned by the presence of concretions [166]. The remains of the allantoic duct, or urachus, which had been obliterated at an early period, may be demonstrated in the umbilical cord.

Of the Placenta and Umbilical Cord.

§ 81. We have already seen (§ 72 and 73) that the chorion is at first covered with villi nearly to the same extent over every part

[165] Many writers, and, among the number, Jo. Müller (in Meckel's *Archiv*, 1830), speak of such concretions. Unfortunately, one which I had, myself, found within the allantoic duct, as it passed into the chorion, was lost by the chemist, to whom I had sent it for analysis. I have filled the allantoic canal distinctly with air, as it lay near the canal of the umbilical vesicle. Two of the figures, 9 and 10, of Baer's tab. vi. appear to refer to this point. The particulars, stated in the text, are all based on my own researches.

[166] Von Baer has descanted at some length on these vesicles in the course of the umbilical cord; and has represented in the fourteenth fig. of his pl. vi. He also refers to the figure of Seiler, tab. x. as exhibiting the same subject. Pockels has described and figured one of these bladders, under the name of erythrois; Seiler has done the same thing under that of allantois. In regard to the formation of the allantois in man, Von Baer holds one of two modes possible; either the lamina vasculosa is raised from its original situation, and applied in the form of a membrane to the outer membrane of the ovum (the chorion), and more or less to the amnion also, or there is no division according to its component layers; but the vessels, as soon as the allantois has reached the outer envelope of the ovum, shoot into and find a nidus in this, when the allantois, now become superfluous, increases no farther. The latter, Baer is induced, from his researches, to regard as the more probable mode of formation.

of its surface, and that these villi become concentrated, as it were, in the course of the third month, upon a particular part, where they grow with great luxuriance, the rest of the chorion becoming in the same proportion smooth. The concentration of the villi occurs in consequence of the production of vessels in the interior from the allantoic layer of the chorion—the endochorion; it is, in fact, only at the place where the umbilical vessels are particularly developed, that the villi increase continually in size, and this usually occurs in the situation where the decidua vera is reflected to become the decidua reflexa. Vessels are also originally developed over the superficies of the chorion in general, and penetrate with its villi into the decidua; but they soon shrink and disappear. As additional matter is poured out by the walls of the uterus at the part where the vessels and villi are especially enlarged, a thickening takes place, which has been spoken of under the title of the decidua serotina; and this gives origin to the PLACENTA, a more or less regularly circular, discoidal, and well defined mass towards the end of pregnancy. The maternal blood-vessels enter freely into this formation; the arteries appear to pass quickly into capacious veins, having very thin parietes, by which a tissue or network of capillaries of extremely wide calibre is produced, amidst which the vessels of the embryo ramify. The two umbilical arteries run tortuous along the elongated navel-string, divide into large branches upon that surface of the placenta which is turned towards the membranes of the ovum, and then plunge along with the villi into the substance of the mass; they run still tortuous in the hollow di-

FIG. CXVIII.

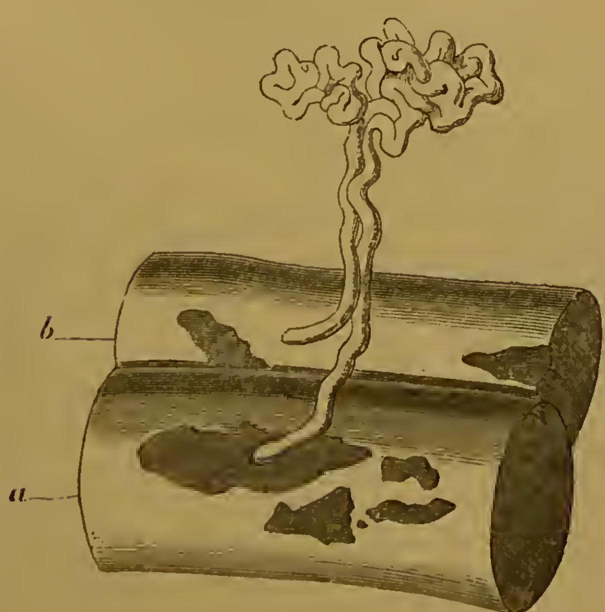


Fig. CXVIII.—A very small and extremely simple villus from the fœtal portion of the human placenta, the vessels of which have been successfully injected. An instance of the kind in which the origin of the capillary vessel distributed to the villus is seen, is extremely rare: *a*, the artery; *b*, the vein.

visions of the villi to their blind extremities, and then turn round and terminate in the veins. Occasionally a delicate arterial twig is seen proceeding from a larger stem (fig. CXVIII.), and terminating almost immediately in a vein, which in its turn runs to join a larger venous trunk. Such simple terminal nooses of arteries in veins are rare; the arterial trunks more commonly divide and subdivide again and again, by which dendritic formations are produced of the same extent as the villi. The different venous roots collect like the arteries on the embryonic aspect of the placenta into larger and larger branches, and finally pour their tide in common into the umbilical vein, which, after tracking the umbilical cord, enters the body of the fœtus, and here terminates in the hepatic vein, close to the trunk of the vena cava inferior. These embryonic vessels have nowhere any direct communication with the vessels of the mother; besides their own parietes the two sets of vessels have always a layer of the chorion interposed between them (fig. CXIX.). The maternal vessels surround the villi of the chorion with their included embryonic vessels, in a continuous but perfectly distinct rete, which, however, appears to be composed of extremely delicate canals, with a wide internal diameter—at least as regards the veins [167].

[167] Weber is the modern anatomist who has investigated with the greatest care the structure of the placenta, and the mode of division and distribution of its blood-vessels—matters of great interest as regards the explanation of the way in which the fœtus is nourished. Vide his edition of Hildebrandt's *Anatomy*, iv. p. 495 et seq. Here, as well as in every manual of anatomy, a particular

Fig. CXIX.

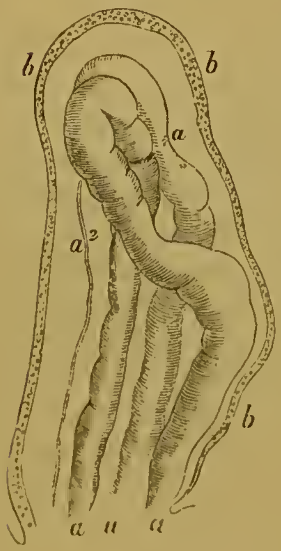


Fig. CXIX.—Termination of a villus of the chorion, from a ripe and perfectly recent placenta, the vessels still filled with blood, magnified two hundred and ninety times. The vessels, *a*, *a*, *a*, are full of blood; the one a^2 is empty. They measure from the $\frac{1}{100}$th to the $\frac{1}{120}$th of a line in diameter.—*b*, *b*, Pellucid margin of the villus.

Summary view of the morphological development of the Human Embryo.

§ 82. The observations now communicated upon the development of the ovum and embryo of the human subject, though they cannot

account of the structure of the navel-string will be found, a subject which does not properly pertain to an elementary work on physiology. Weber's views have given occasion to a good deal of controversy, and I here present an extract from the manuscript communication of that able anatomist, supplied to me for the purpose of publication. He says: "Eschricht of Copenhagen, in an interesting academical tract entitled, *De Organis quæ respiratione fœtus Mammalium inserviunt, Prolusio Academica,* Hafniæ, 1837, 4to, shows that he agrees with me in many points in regard to the structure of the placenta of man and animals, whilst on others he proclaims his dissent. The particulars in which he agrees with me are the following. 1st. That the arteries and veins of the uterus, the channels of the mother's blood, penetrate in great numbers into the placenta, and are distributed throughout its substance in such wise, that every one of its minutest lobules has a canal carrying the blood of the mother, and so comes into contact with the vessels in which the blood of the embryo is flowing. Here we both differ from Seiler, who believed himself authorized to conclude that no vessels from the mother penetrated the placenta, but that the maternal vessels only came into contact with the surface of the placenta, where it was bounded by the uterus. 2d. The umbilical arteries of the embryo divide, in the manner of a tree, into very numerous and minute branches, which finally turn round, forming loops and anastomoses, and again collect into larger and fewer branches, which at length unite into a single trunk, and form the umbilical vein. No where do the maternal and fœtal vessels anastomose; no where is there any transmission of blood from the one class of vessels to the other; no where do we encounter open-mouthed terminations of vessels. 3d. The whole placenta, and therefore every individual lobule entering into its structure, consists of two distinct parts, the one a continuation of the chorion and vessels of the embryo, the other a continuation of the membrana decidua and vessels of the uterus. From the chorion, for instance, dendritic processes or elongations are sent out, which in small ova about a month old are so small and simple, that they are called villi, but which grow by and by into large and numerously divided stems and branches. Into each of these dendritic processes of the chorion there penetrates a branch of the umbilical artery, and a branch of the umbilical vein. Both vessels divide into branches in the same manner as the process of the chorion in which they run. At the extremities of the branched processes of the chorion, the divisions of the umbilical artery come together in loops or coils; these coils, however, are for the most part not simple; the same capillary winds several times hither and thither, and forms several loops; loops are also frequently formed by the anastomosing of two neighbouring capillaries. From these convolutions and loopings of the capillaries, little thickenings or enlargements of the extreme divisions of the processes of the chorion are produced. Each particular trunk, with its divarications of the shaggy chorion, forms a lobe or lobule of the placenta, which is covered by the tunica decidua. To this investment many of the terminal branches of the chorion will be found to have grown. It is in the spaces between the divarications

be viewed otherwise than as fragmentary, still bear so striking a resemblance to the evolution of the mammalia and birds, that the

of the chorion, that those vessels run which transmit the blood of the mother, and which are prolongations of the uterine arteries and veins; they penetrate in this way to every the most minute lobule of the chorion. 4th. The object of this structure seems to be that the minute, convoluted, greatly elongated, and extremely thin-walled capillaries, in which the blood of the fœtus is circulating, may be brought into the most intimate contact possible, with the larger but everywhere excessively thin-walled canals, in which the blood of the mother is flowing, that the two currents, without interfering with each other's motion, may pass each other to as great an extent as may be, with nothing interposed but the delicate parietes of each set of vessels; that they may exert an influence one upon another, the blood of the mother abstracting matter from that of the fœtus, and the blood of the fœtus taking, in its turn, matter from that of the mother. Eschricht differs from me in this, that he believes the uterine arteries and veins distributed to the placenta are connected together by as delicate, or even a more delicate system of capillaries, as that of the umbilical arteries ; and in such a way that two systems of capillaries, that belonging to the child to wit, and another to the mother, are brought into intimate contact. I, on the other hand, believe I have demonstrated that the uterine arteries and veins, once they have entered the spongy substance of the placenta, do not farther divide into branches and twigs, but immediately terminate in a network of vessels, the canals of which are of far too large diameter to permit them to be spoken of as capillaries, and of which the parietes are so thin, that they cannot be shown apart by the most careful dissection. This vascular rete, which connects the uterine arteries and veins with each other, completely fills the spaces between the branched divisions of the chorion, and the extremely thin parietes of the canals of which it is composed, insinuate themselves at all points into the most intimate contact with the branches and convoluted masses of the capillaries of the umbilical system of vessels. This network of vessels, however, with reference to the passage of the uterine arteries into the uterine veins, performs the same office as a rete of true capillaries, so that it may be regarded as a rete of colossal capillaries. Eschricht maintains that plicated processes of the decidua penetrate the placenta, and may be traced between the branched divisions of the chorion, furnishing the several twigs with a delicate investment, and that these plicæ are the supporters of a capillary rete, by which the uterine arteries and veins are connected in the placenta. I, on the other hand, maintain that the walls of the uterine arteries and veins, where they penetrate the placenta, consist of a very delicate tunic, a prolongation, as it seems, of the inner tunic of the vessels of the uterus, covered with a layer derived from the substance of the decidua ; that the inner tunic of the blood-vessels lines the interspaces between the divisions of the shaggy chorion, and that the little masses of convoluted vessels or villi, which terminate the branches of the chorion, penetrate the canals which transmit the blood of the mother, and are bathed by it in their interior. In my mode of stating my views, I must, I fear, have left room for misapprehension, as I could perceive in the course of my conversation with Eschricht, that I had not been understood in the way I intended. I have not, I imagine, explained with sufficient clearness what I mean by *villi that penetrate the vascular canals of the mother.* This deficiency I

account of the development in these classes of animals may be assumed as affording unobjectionable data in regard to that of man;

take occasion to supply here. I do not then understand by villi entire stems of the chorion with all their subdivisions, as they appear when they are torn forcibly out of the placenta, but small projections or elevations that occupy these in points, or occur over every part of the stems and branches, and are formed by the terminal loopings and communications of the embryonic placental capillaries. Magnifying glasses are required to perceive these proper villi distinctly. In the second place I have said: 'the vessels of the uterus that penetrate the placenta become wider when they have entered it.' This expression is objectionable, at least in reference to the veins of the fully developed placenta, and I would therefore recall it." Weber then goes on to describe the structure of the placenta particularly, comparing it with the *corpus cavernosum penis* s. *urethræ*, or with an ordinary sponge. "The fibrous tissue of the sponge," he continues, "corresponds with or represents the branching subdivisions of the chorion and their uniting medium derived from the decidua; the cavities and interspaces of the sponge, however, represent the passages in which the blood of the mother flows. None of the many tortuous arteries which penetrate the decidua, still dividing into branches, from the uterus, when they reach the placenta undergo any farther subdivision; they open at once into the spongy texture, and are lost as ordinary vessels. Neither do the veins show any thing like division into branches; they all open like the arteries into the spongy substance of the placenta, by orifices larger or smaller. It is only as they are running in the investing decidua that they divide into a few branches. The spaces between the branched subdivisions of the chorion are thus kept filled with blood constantly poured in by numerous and large arteries, and regularly carried off again by numerous and capacious veins, so that it is perpetually renewed." Weber now details the grounds of his conclusions, which rest on injections of the uterus and other parts of women who have died in their pregnancy, on researches made on the recent after-birth, and on the study of smaller and fresh human ova. He remarks, among other things, that "if the uterine surface of a very fresh placenta, that has not been put into water, be moistened with a strong solution of corrosive sublimate in alcohol, in order to coagulate and prevent the escape of the blood still contained in it, and the whole placenta be then soaked in a weaker solution of the same kind, the whole of the maternal blood that remained in the spaces between the divisions of the chorion will be found coagulated; even in the larger lacerated veins that have just passed from the uterus into the placenta, coagulated blood will be found; and the manner in which these veins open into the interspaces mentioned, will be seen, and the course of the maternal blood during life be found indicated." Weber's observations on the structure of the placenta in the Mammalia are also extremely interesting; but as they extend to a considerable length, and a notice of them has already appeared (in Froriep's *Notizen*, Oct. 1835), I shall not enter upon them here. The placentas of all animals seem referable to two grand classes: "But the nourishment of the embryo appears in every case to depend on the subdivision of the fœtal and maternal blood into innumerable currents, the fœtal blood being however subdivided much more minutely than that of the mother, which pass each other through a great extent of tube, and are in contact through a like or still greater extent of surface, but always

with the materials drawn from thence, we may, without any risk of real error, attempt a connected sketch of the entire subject.

without the stream of the one interfering with that of the other, and without any admixture of the blood of the mother with that of the fœtus. These currents are

Fig. CXX.

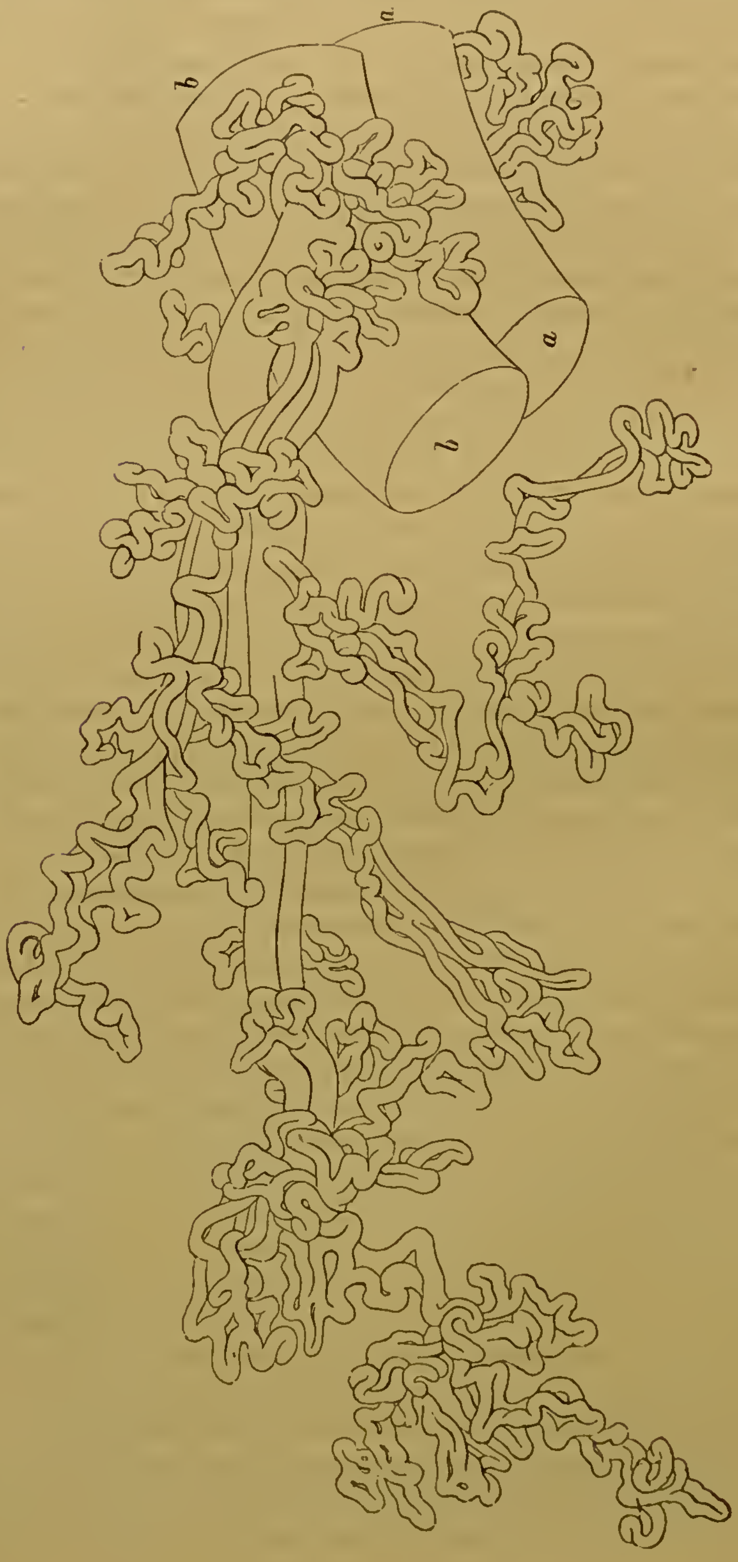


Fig. CXX.—Villi from the fœtal portion of the placenta, at the full time. The capillary vessels are filled with injection; their diameter varies from the $\frac{1}{115}$th to the $\frac{1}{170}$th of a Paris line. The preparation is dry, and is seen magnified about 100 times: *a*, the artery; *b*, the vein. The drawing communicated by Dr. E. H. Weber, of Leipzig.

The structure of ovarian ovum, and of the Graafian vesicle, the formation of the corpora lutea, are in man precisely as they are in animals; so that there can be no doubt of the ova quitting the

in fact separated from each other at every point, by parietes of extreme thinness, which, however, do not oppose all interchange of matters, these transuding or making their way through the delicate bounding membranes." Baer (*Entw.* S. 279) says: "By the growth of the vessels of the uterus into the decidua serotina, this is transformed into the placenta. That vessels pass from the walls of the uterus into the placenta is a fact long known and admitted; but in regard to the form and mode of this passage or transference, opinions still vary. It was long believed, with Hunter, that they passed into cavities. In more recent times there appeared a growing disposition to regard these spaces as enlarged veins with extremely thin walls, a structure which is assigned to them among others and particularly by E. Weber. Very lately, however, Dr. R. Lee has very emphatically insisted, that the great veins of the uterus ended open-mouthed on the inner surface of that organ, but that these openings were closed by the substance of the tunica decidua, and that generally no other than vessels of very small calibre penetrated the decidua from the uterus. I myself used to view the matter as Weber has represented it; and since the statements of Lee, I have had no opportunity of appealing to nature for a solution of the question." I have myself discovered a very easy and simple method of procuring satisfaction, in regard to the structure and course of the embryonic vessels, without the assistance of any sort of injection. Let the smallest possible piece or lobule be removed by means of scissors, or forceps, from the uterine surface of a fresh placenta (which must by no means have been macerated in water), immediately under the delicate covering of the decidua, and this, covered with a delicate plate of glass, be brought under the microscope. The villi of the chorion will be seen full of the vascular coils of the embryonic vessels injected with blood (figs. CXIX. and CXXI.). These vessels are all of considerable size; I found them from the $\frac{1}{100}$th to the $\frac{1}{120}$th of a line in diameter, often nodulated as in the Malpighian bodies of the kidney; the flocculi of the chorion surrounded them more or less closely, but sometimes so loosely (fig. CXIX.), that a clear crystalline space remained between the walls of the vessels and the bounding membrane of the villi, which were about the $\frac{1}{300}$th of a line in diameter, and showed on their edges a granular or cellular structure. Some vessels I observed much finer than the generality, not more than from the $\frac{1}{200}$th and $\frac{1}{250}$th of a line in diameter (fig. CXXI.); and in

FIG. CXXI.

Fig. CXXI.—Vessels of the same part of smaller diameter, examined in the same manner. The vessels, *a*, *a*, the parietes of which are especially distinct at *a* ², are seen thickly filled with blood globules, which lying face to face form columns; *b*, *b*, edge of the villus, here lying close to the vessels in their course; the vessels measure the $\frac{1}{200}$th of a line in diameter.

ovaries, descending along the Fallopian tubes, and reaching the uterus precisely as in the mammalia (§ 69). With simple analogy for our guide, we may conclude that the ovum reaches the extremity of the tube between the eighth and fourteenth day. The uterus at this time is already lined with the tunica decidua (fig. CX. *c*). If the ovum (fig. CXI. *g*) now passes from the orifice of the tube (fig. CXI. *b*) into the uterus, it will, as a general rule, glide between the wall of the uterus and the tunica decidua, push this away from its connexions with the uterus, and carry it forwards or inwards (*e*, *e*), by which the decidua reflexa is formed. The ovum now hangs within a sort of pouch into the (fig. CXI. *d*, enlarged) internal cavity of the uterus, which diminishes in extent with the growth. The cavity of the uterus is usually open at this period, the cervix uteri (fig. CX. and CXI. *a*) not being as yet closed up by its plug of gelatinous matter (§ 77). As soon as the ovum has reached the cavity of the uterus, it must grow rapidly by attracting matter from the fluids around it, and soon become readily visible to the naked eye; the granular disc about the chorion is resolved; the chorion itself has expanded and become thinner (CXXII. *a*). The vitellary ball (*b*) appears to be completely

these the globules of the blood presented a very beautiful appearance, the vessels being but of a diameter to a single row, so that they were arranged in parallel columns. The hem or margin is seen running close to the vessels (fig. CXXI. *b*). With regard to the maternal vessels, I could not make out anything clear or satisfactory. Von Baer's congratulatory address to Soemmerring, which treats "Of the vascular connection between the Parent and Embryo" (*Ueber die Gefäss-verbindung zwischen Mutter und Frucht*) Lips. 1828, fol. may be referred to for farther information on this subject. [Dr. Lee's paper, "*On the Structure of the Human Placenta and its connexion with the Uterus,*" will be found in the *Phil. Trans.* for 1832. This zealous inquirer has seen reason to alter his opinions there stated. He now admits that the maternal blood enters the cells of the placenta by the tortuous arteries in the decidua, and is returned into the uterine veins by oblique openings in this membrane. R. W.] Ritgen's work, "*Contributions to illustrate the mode of connexion between the human Embryo and the Uterus*" (*Beiträge zur Anfhellung der Verbindung der menschlichen Frucht mit dem Fruchthälter*, &c.) Lips. and Stuttg. 1835, fol. does not advance the subject beyond the degree in which it was already known.

Fig. CXXII.

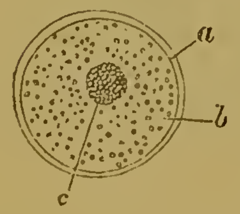


Fig. CXXII.—Human ovum, which had reached the uterus, greatly magnified. The external tunic *a*, surrounds the internal vesicles, the vitelline, to wit, and the germinal, *b*, upon which an aggregate of granules, *c*, the embryonic spot, indicates the point of formation of the future embryo. Vide fig. LXV. in the dog.

grown round by the blastoderma or germinal membrane, betwixt which and the chorion a thin layer of albumen appears now to have been deposited (§ 70); the vitellus has become more diffluent, and a round pretty thick granular cumulus, which is to be regarded as the central part of the blastoderma, has been formed. Of these particulars, we derive our information from the dog and the rabbit (§ 70, and figs. LXV—LXX); and there can be no doubt but that matters go on precisely in the same manner in the human subject. In the perpendicular section (fig. CXXIII.) of the ovum at this period, *c* would be the thickened granular cumulus, from which the development of the embryo commences. This granular mass will become clearer in the middle with the progress of the development; and, as in the bird (§ 50, and tab. CXI. figs. XXV—XXVIII.),

Fig. CXXIII.

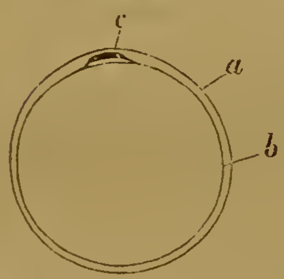


Fig. CXXIII.—Perpendicular section of an ovum similar to that of last figure but somewhat longer: *a*, chorion; *b*, vitelline vesicle (vitellus); *c*, the serous lamina of the germ.

Fig. CXXIV.

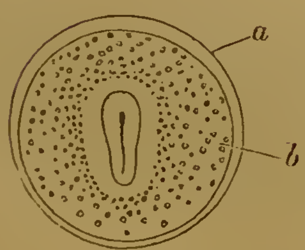


Fig. CXXIV.—An ovum still farther advanced. The embryonic spot is thinner and more transparent. Within the oval area vasculosa is situated the pyriform area pellucida with the nota primitiva in its middle; *a*, chorion; *b*, vitellus. Contrast the appearances presented by the embryo of the fowl, fig. XXV. and XXVII. and in the dog, fig. LXXII.

Fig. CXXV.

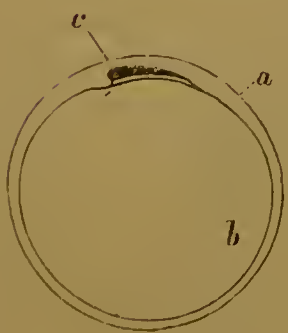


Fig. CXXV.—Perpendicular section of the ovum of last figure: *c*, lamina serosa.

and in the dog (§ 71, and figs. LXXI. and LXXII.), an oval form of blastoderma ensues, in the middle of which lies the transparent pyriform area proligera with the primitive streak (fig. CXXIV.). In the circumference of this the area vasculosa is developed, and the vitellary globe or mass (*b*) now completely enclosed by the blastoderma, has detached itself to a greater extent from the smooth chorion (*a*). The rudiments of the embryo (fig. CXXV.) are seen as a thickening of the serous layer (*c*), which is now parting from the underlying mucous layer. Analogy with the embryo of the bird and quadruped leads us to infer that the formation of the serous envelope and of the amnion (fig. CXXVI.) in the human subject proceeds exactly in the way we have found it to do in these lower animals (§ 56), and that the embryo (fig. CXXVI. *c*) is surrounded by a cranial (*d*) and a caudal involucrum (*e*), precisely in the same way; by this development of the peripheral portions of the serous layer, the embryo, which is becoming more and more strongly curved, is pinched off in a greater degree from the vitellicle or umbilical vesicle (*b*); the vascular and mucous layers (fig. CXXVI.) are to be distinguished as superimposed laminæ in the abdominal cavity,

Fig. CXXVI.

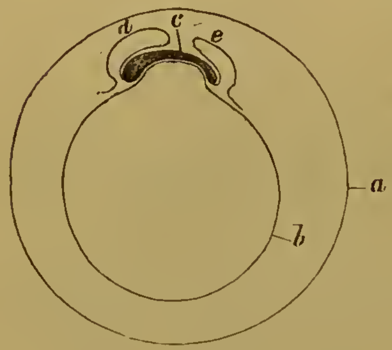


Fig. CXXVI.—Human ovum still farther advanced. Perpendicular section. The embryo *c* is curved in a greater degree, and is formed of the three laminæ of the germinal membrane; the vitellicle, the future umbilical vesicle, *b*, begins already to be pinched off, as it were, by the convergence of the opposite ends of the embryo; the amnion and serous lamina form the involucrum capitis *d*, and the involucrum caudæ *e*.

Fig. CXXVII.

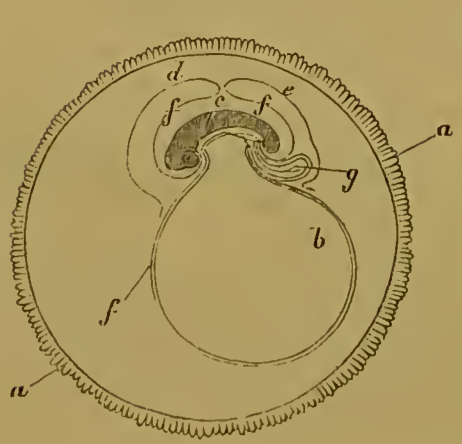


Fig. CXXVII.—Human ovum still farther advanced. The chorion, *a*, *a*, has now produced villi in abundance; the umbilical vesicle, *b*, is grown over by the lamina vasculosa *f*; from the embryo *c*, the amnion *f*, *f*, and the lamina serosa *d*, *e*, are detached, and meeting over the back of the embryo they will soon coalesce. The allantois, *g*, has been produced, and is covered with vessels.

the latter having at an earlier period completely overgrown the vitellicle. At a later stage in the development (CXXVII.) the villi become more conspicuous as formations sprouting from the outer wall of the chorion (fig. CXXVII. *a*); the serous envelope (*d*, *e*) rises from the amnion (*f*, *f*) whilst the two folds composing the involucrum of the head (*d*) and the involucrum of the tail (*e*) meet and grow together; the vitellicle or umbilical vesicle (*b*) is surrounded by the vascular (*f*) as well as the mucous layer. In the cavity of the abdomen, the rudiments of the principal viscera have now been formed by the extension and folding in of the two layers; the allantois (*g*) has pushed forwards betwixt the amnion and serous layer; the embryo is still more strongly bent, and still farther separated from the vitellus. The albuminous space within the chorion has enlarged greatly. As soon as the serous layer (fig. CXXVIII. *h*) is completely detached, it is pushed in the albuminous space against the inner wall of the chorion by the increasing amnion (*f*), and there apparently forms, in part at least, the tunica media, as it is entitled; the arachnoidal tissue of the albuminous space is also to be regarded as partially composed of coagulated albumen (§ 78. Annot. 156). The amnion is developed at an early period in the human subject, and soon surrounds the embryo in the guise of a capacious bag. On the chorion the villi become concentrated, as it were, towards a particular spot (*k*, *k*), and here the placenta is by and by formed; other places, on the contrary, become smooth (a^1), or are covered with shorter villi (a^2). The allantois (*g*) has now acquired the form of an elongated vascular sac, and is applied to the chorion—it has indeed at this period completely grown to the chorion; it is only represented as it ap-

Fig. CXXVIII.

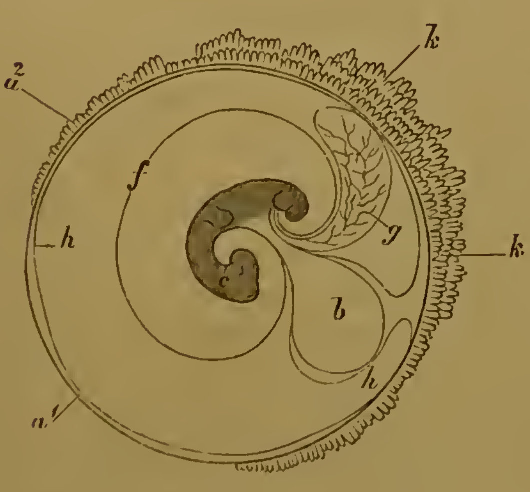


Fig. CXXVIII. — The human ovum in a state of still greater advancement. The chorion is now smooth at one part a^1; elsewhere it is villous, especially about *k*, *k*, where the placenta will be formed; the amnion, *f*, already surrounds the embryo, *c*, in the guise of a spacious bladder; and the serous envelope, *h*, *h*, has become applied to the inner aspect of the chorion; the allantois, *g*, is at the same time applied to the chorion, and the umbilical vesicle, *b*, is now smaller, and its neck becomes narrower and longer.

pears in fig. CXXVIII. *g*, for the sake of making the strueture plain. The vitellus (*b*) has at this epoch beeome a pediculated pyriform vesicle—the umbilieal vesicle, upon which the vessels have shrunk; the head of the embryo (*c*) is now found to have sunk greatly downwards in almost all ova. At the beginning of the third month (fig. CXII.) the os uteri is seen filled with a consistent gelatinous plug (fig. CXII. *a*): over the os uteri the deeidua vera is generally wanting; it lies elose to the walls of the uterus (*c*, *c*), sends out on that side where the ovum has not entered, shorter or longer proeeesses (c^2) into the orifice of the Fallopian tube (*b*); but here too it is frequently perforated or absent (§ 77); the decidua is deeply inverted or involuted by the ovum (fig. CXI.), so that it is only inferiorly (*d*) that there still remains any spaee between the decidua vera and decidua reflexa; the edges of the involution (*e*, *e*), the eircle where the true and the reflected deeiduæ pass the one into the other, ean be followed; the interval that was produeed by the separation of the deeidua becomes filled with a new exudation (*f*), and in this way is the decidua serotina formed; at this part also the villi of the chorion are additionally evolved by the pressure of the allantois (*g*) upon them. The allantois terminates in the uraehus and bladder; near the urachus lies the pedicle of the umbilical vesiele (h^2) in the umbilical cord; the umbilical vesicle itself (*h*) is ineluded in the space betwixt the amnion and chorion; through the compression of the albumen, the membranous stratum (i. e. the tuniea media united to the serous covering) is readily demonstrable as a distinct coat.

CHAPTER III.

OF THE DEVELOPMENT OF THE TISSUES (HISTOGENY).

Materials.

§ 83. In our exposition of the development of the chick, and aeeount of the human embryo, a merely general and relative view of the morphologieal changes undergone has been taken; not to interrupt the narrative, the mode in which the tissues originate (histogenia), and the doetrine of the intimate structure of these and of the organic parts at large (histologia), have been only touehed upon by the way, and incidentally. In the present chapter, it will be our business to make good these deficiencies.

The knowledge we possess in regard to the earliest formations of the tissues has been especially derived from the study of embryos of the mammalia and man, recourse being, at the same time, had to the incubated egg, more particularly during the earlier periods of its transformations [168].

Structure of the germinal Membrane (*Blastoderma*).

§ 84. So soon as the germinal membrane is formed in the hen's egg, a change or metamorphosis is seen to have occurred in its constituent globules or cells, which, even in the sixteenth hour of incubation, show a difference of form in the serous and mucous lamina. In the *serous* stratum, the cells tend to protrude outwardly, in the form of hemispheres, and by pressing closely one upon another, they acquire the appearance of six-sided figures (fig. CXXIX.); each cell contains a distinct nucleus, in contact with the inner aspect of its walls, of a round shape, and itself showing one or two nucleolar molecules; the cells are, moreover, distended with a transparent fluid, in which, however, small granules appear, which, still included in the cells, exhibit molecular movements. In the *mucous* stratum, the cells are particularly large, and, under the microscope, resemble little yolks, including granules and globules of very various dimensions (fig. CXXX.) One or more of these globules are larger than the rest, and show a darker contour; the other globules exhibit a finely granular mass having molecular movements, suspended in a transparent fluid. These cells or globules lie rather loosely together in a thick intercellular substance, but without visible structure, as their cytoblastema [169].

[168] Much information on the subject of histogeny will be found in Valentin's *Account of the Evolution (Entwickelungsgeschichte)*, and in the work of Schwann, already so frequently quoted, *Microscopical Investigation of the Accordance in Structure, &c.* Berl. 1838. In the paragraphs that immediately follow, I have preferred laying the observations of Valentin and Schwann before my reader, to using any of my own, my researches in histogeny being of too fragmentary a character, and not agreeing in every particular so entirely as I could have wished with those of the excellent observers mentioned, who have made this subject their particular study.

[169] The account just given is especially after Schwann (loc. cit. p. 65). Valentin, however, was perfectly well aware of the histological differences in the two laminæ of the blastoderma, and gives the dimensions of the globules, or cells as they are now regarded; those of the lamina serosa, which, by mutual compression assume the form of six-sided bodies, he compared to the cellular tissue of vegetables. In the spring of the year 1838, I observed the differences specified with great distinctness in the several laminæ of the germinal membrane,

Formation of the Blood and Blood-vessels.

§ 85. The earliest stages in the formation of the blood, and of the blood-globules and vessels, are extremely difficult of observation; and no one of the many who have given their especial attention to the earliest stadia of evolution generally, has succeeded in completely following the process of their evolution through all its stages. As we have seen, the formation of the blood in the embryo of the mammal, bird, and frog, occurs at a very early period. The cells which lie between the serous and mucous lamina of the blastoderma comport themselves in a peculiar manner in the chick, even

represented in fig. XXVIII., and made drawings of the appearances in the three strata *b, c, d.* The globules or cells of the mucous lamina appeared to me precisely as Schwann has figured them; in the serous lamina, however, I was only aware of the existence of small granules, probably the nuclei of the cells, overlooking their envelopes. At this time, Schwann's researches were still unknown to me; at the present moment (Nov. 1838,) I have no opportunity to examine the subject anew.

Fig. CXXIX.

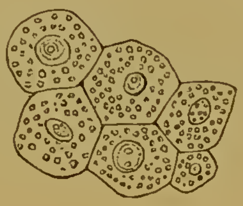


Fig. CXXX.

Fig. CXXXI.

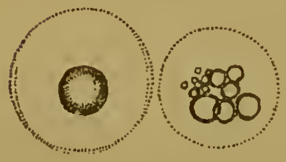


Fig. CXXXII.

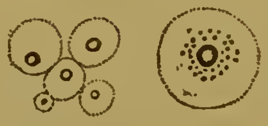


Fig. CXXIX.—Cells of the lamina serosa of the blastoderma, with their nuclei. Fig. CXXX. cells and globules of the lamina mucosa. Fig. CXXXI. globules of the vitellus. Fig. CXXXII. globules of the thinnest part of the vitellus from the central cavity of the part. These figures illustrate the cellular structure of the blastoderma and vitellus, according to Schwann, (see his microscopical investigations of the accordance in structure, and mode of growth among vegetables and animals, tab. ii.)

so early as the 20th hour from the commencement of incubation; they appear to be very loosely connected, and form a spongy lamina, which seems to imbibe a great deal of moisture, derived principally, as it would seem, from the central cavity of the vitellus, and the canal that ascends from it to the germinal membrane (§ 47, fig. XVI. *i*, *k*, p. 47). A certain proportion of the globules or cells appear to be transformed into blood-globules; perhaps the nucleus of the cell affords the rudiment of the nucleus of the blood-globule, for this is extremely distinct at the very earliest periods; the blood-globules too of the embryos of both animals and man are, for some considerable time, notably larger than those of the adults of the several kinds. Another portion of the cells or globules of the vascular lamina, by becoming applied to one another form the parietes of the blood-vessels. The walls of the heart in the chick, towards the end of the second or beginning of the third day, can be seen to be constituted by a union of many polyhedral cells, each of which presents a darker spot in its middle, undoubtedly the nucleus of the pre-existing and unconnected cell (fig. CXXXIII.). In a precisely similar way are blood and blood-vessels formed in the periphery, as in the centre. The blood, at first, is colourless, but it begins to acquire colour so early as the end of the first, or beginning of the second day, at which period it may be seen moving in circumscribed vascular channels, under the influence of the undulatory action of the heart[170].

170 The formation of the blood will be treated at greater length by and by; here I have only given the most general and essential points, after my own observations; the results of the researches of Pauder, Baer, Valentin, Baumgärtner, Reichert, and others, will be stated in the Second Book of this work, which treats of Nutrition. On the singular difference in the size of the blood-globules in young embryos and adult individuals of the same kind, first observed by Dr. E. H. Weber and myself, see my *Contributions* (*Beiträge, &c.* 2tes. Heft, S. 35). This difference deserves mention in this place, as it affords a new assurance against the existence of any direct communication between the vessels of the mother and those of the embryo.

FIG. CXXXIII.

Fig. CXXXIII.—The heart of the embryo of the fowl, end of the second day, greatly magnified. The cellular structure of the parietes of the organ is apparent; each tessellated cell has its nucleus. The several divisions of the heart are also already indicated; *a*, the atrium; *b*, the ventricle; *c*, the bulb of the aorta.

Origin and Evolution of the Tissues.

§ 86. The present state of our knowledge of the histogenesis, or doctrine of the formation of the tissues, renders it probable, that all the tissues result from metamorphoses of the primordial cells of the germinal membrane and vitellus. The first indications of histological difference appear in the three laminæ of the germinal membrane, which then immediately afford the elements of all the succeeding tissues. The structure of these tissues will fall under consideration by and by, in the particular appropriate sections of the different books of this work; in the following annotations, the history of the development of the several tissues will be found sketched in general and broad outlines.

Professor Valentin at my request has furnished me with a general survey of the subject of histogeny, which I communicate here entire, and as it came into my hands.

PRINCIPAL FEATURES IN THE DEVELOPMENT OF THE ANIMAL TISSUES, BY G. VALENTIN.

In my first histogenetic inquiries, I observed certain peculiar granules embedded in transparent gelatine, as the elementary matter of all the tissues. I remarked the difference between these granules in the serous and mucous laminæ, at the period of the earliest separation of these layers from one another. In the vascular lamina I found large globules or cells, which in form and mode of mutual apposition I likened, so long ago as the year 1835, to the cellular tissue of vegetables (*Entwickelungsgeschichte*, 287). I also first directed attention to the resemblance in form and appearance of the cartilages beginning to be ossified, particularly of the branchial cartilage in the larva of the frog (from observations made in conjunction with Purkinje), to the cellular tissue of plants (*ib.* 209, 210). I described the round cells of the globules with their interposed cellular substance, of the chorda dorsalis of young embryos (*ib.* 157, and *Repertor.* i. 187). Shortly after this, I. Müller, from his own independent observations, announced the cellular structure of the chorda dorsalis of fishes (on the *Myxinoids*, 74). In the Epithelium, which Purkinje and Raschkow (*Melet. c. mammal. dent. evolut.* 12), as well as myself (*Nov. Act. Ac. N. C.* vol. xviii. p. i. 96), compared to the cellular tissue of plants, I chose, expressly on account of this resemblance in form, the same designation for the central mass, viz. nucleus, just as I subsequently described the nucleolus which was observed by me at a later period (*Repertor.* i. 143). In the study of the Epithelium continued particularly by Henle and me, the analogy to the cellular tissue of vegetables could not be missed, and the independence of the cellular parietes was distinctly indicated (*ib.* i. 284). I had also seen that the nuclei were the parts first formed in the pigment of the choroid coat of the eye (*Entwick.* 194), and I compared the pigmentary cells to the vegetable cellular

tissue (*Repert.* 245, *Langenbeck, de Retina*, 38). Schwann gave undoubted completeness to these analogies when he showed that the gelatinous primordial mass of the tissues was composed of cells, that the granules or bodies embedded in it are nuclei, and that these often exhibit laws of evolution of the same kind as the cells (Frorieps, *Neue Notizen*, Heft i. 3, 1838, and *Micros. Untersuch. über Einstimmung*, &c.) In 1837, I had observed the cells of the germinal membrane in the ovum of the Sepia, with their nuclei and nucleoli, and the areas that surround them, and made known my observations in a letter to Breschet. Very shortly after I became acquainted with Schwann's first paper (Frorieps, *N. N.* 1838), I began a series of observations on the subject; and the chief results of these my more recent investigations form the matter of the following communication. I have at the same time referred at the proper places to Schwann's "Inquiries" (*Untersuchungen*, &c.), the first part of which I have this day received.

As among vegetables so among animals we find granular nuclei, including one or more nucleoli and surrounded by more or less independent cells, which consist of separate bounding parietes, and distinct contents. From this primordial formation proceed all the tissues, how heterogeneous soever they appear in their completely elaborated and perfect estates. The different ways by which the metamorphosis happens are susceptible of arrangement in an ascending series, under the following elementary types :—

I. *The nuclei with their nucleoli, which at an earlier stage are free, surround themselves with a clear cell, which however soon dissolves, so that the nuclei swim about as characteristic corpuscules in the fluid, and there and as such advance in their individual development.* In the normal organism this is what happens in regard to the *Blood*, and probably also to the *Lymph.* The blood-globules are not cells, but nuclei. Their nuclei are in effect nucleoli. This view is vouched for by two decisive facts :—1. In the larvæ of frogs we see plainly round or square shaped granules, applying themselves around the nucleoli (*Enwickelungsgesch.* 297. Wagner, *Beiträge*, Heft ii. 38), and by and by transforming themselves into a homogeneous shell, whilst the nucleus remains. This is the type of the mode in which the nucleus universally originates, and attains its development, whilst the cell around the nucleus appears without exhibiting any transition-stage of the kind. 2. When the blood-globules of the embryo, even after they have attained the flatness that characterizes them in the mammalia, and agree in size with those of the mature animal, are treated with acetic acid, they suffer little or no change in form and size; whilst this acid immediately reacts in the well-known manner upon the fresh blood of the mother. The blood-globules of the embryo thrown into concentrated acetic acid first lose their colouring matter, although in a less degree than when treated with distilled water, and they retain their shell or envelope for two days or more, either crisped or altogether unaltered. Now insolubility in acetic acid is a general character of the nuclei of the blood-globules, whilst the cells and the products of their metamorphoses are universally attacked in a greater or less degree by the acid in question. The bodies called the lymph-granules of the blood, are in all probability free nucleoli, which gradually surround themselves with nuclei. Among the products of pathological states, exudation corpuscules [coagulable lymph granules] belong to this category. Like so many embryonic nuclei these are round, granular, and lie tessellated one upon another, whilst their very small interstices contain a transparent gelatine. Should the exudation become purulent, this gelatine acquires fluidity, and the pus globules then swim in the liquor

puris, sink tessellated to the bottom, and surround themselves with cells, which subsequently undergo transformation in accordance with the laws immediately to be named into exudation-fibres or exudation-membranes.

II. *The nuclei surround themselves with cells which are permanent, but various metamorphoses of both the nuclei and cells ensue, according to the individual character of the tissues and parts which they go to compose:*

(*a*) Epithelium.—In the *Cellular Epithelium* the cells are more or less polygonal, flat, and lie tessellated or pavement-like near one another. The parietes become (from secondary deposition?) granular and horny. The nuclei grow smaller, clearer, often smooth, and lie here centrally, there excentrically; finally, the nucleus often becomes attached to the inner aspect of the wall of the cell. In the *cylindrate epithelium* the uppermost and oldest cell is cylindrical, and its free superior surfaces are either level or slightly convex, its opposite aspect appearing more pointed, and produced into a filament. In the *ciliate epithelium* the free upper surfaces of the cells are beset with cilia, only on their edges however, not on their middles. The nuclei are clear, and when the tissue is treated with water they often present themselves between the cilia, or where these have fallen off they look like clear globules (*Nov. Act. Ac. N. C.* vol. xvii. p. ii. tab. lxv. fig. 3). All the cylindrate and ciliate epitheliums show a longitudinal perpendicular arrangement of cells (*Repertor.* iii. 310).

(*b*) Horny tissue.—As the best example of the horny tissue, I select the hoof of the mammal. The nuclei in this tissue are in the first instance, both relatively and absolutely, large, opaque, round; the cells are relatively small, transparent, and without obvious constituent molecule in their parietes. By and by, both the walls and the contents of the cells expand conspicuously, without losing their half-polyhedral, half-round, characteristic boundaries. The more the cells dilate, the more do the nuclei shrink, and they finally present themselves to the observer as very elegant round corpuscules having one nucleolus, and in extremely rare instances several nucleoli, in their centre. The nuclei from the peculiarity just mentioned and their flatness finally bear the closest resemblance to the blood-globules; they are attached, generally excentrically, to the inner aspect of the parietes of the cells. These parietes are rough (from granules or laminæ applied to the inner aspect of the primary walls of the cells?) and grow constantly more and more horny. The cells often exhibit a certain expansion lengthwise (hoof of the horse), at the same time that they become more transparent and more intimately connected, although here and there their boundaries, even in grown animals, are frequently still to be detected. On other horny tissues, vide Schwann, l c. 90—99.

III. *The cells exhibit metamorphoses, which in point of form are in all respects analogous to those we observe during the formation of the wood, and indeed of the pores, in plants.* (Burdach, *Physiol.* 2 Aufl. B. ii. 168.) At first there arises a polyhedrous cell, with a large opaque nucleus. This nucleus, however, is absorbed, and grows smaller in the same proportion as a deposit furnished with spiral canals takes place on the inner aspect of the wall of the cell. The primary wall of the cell is at all periods readily to be distinguished. The canals in neighbouring cells correspond with one another. The tubular membrane of the crayfish, *Repertor.* i. 124, tab. i. fig. 23, and in all probability the membrane of the enamel of the teeth, are formed in a similar manner.

IV. *The cellular element is extremely distinct in the earliest periods of its formation, but a secondary product obscures it, or even causes it to disappear entirely.*

(*a*) Fat (*adipose tissue*).—The cellular element is most advantageously examined in much emaciated subjects. If the integument covering the pectoralis major muscle be removed, and a very delicate slice of one of the small masses of reddish yellow-coloured fat, which will there be found lying immediately under the corion, be placed in the field of the microscope, a very beautiful series of polyhedral cells with distinct parietes will be brought into view. The periphery of the somewhat pale granular nucleus is generally distinctly visible. A large fat or oil globule occupies its centre, and around it, concentrically disposed but more or less scattered, a variable number of smaller fat globules. Large fat globules, with concentrically scattered smaller ones, and a surrounding transparent but definite cell, are conspicuous in the reddish yellow-coloured fatty mass which lies over the spinal cord of the calf. On the cells of the vitellus, vide Schwann, l. c. 56.

(*b*) Pigment.—I have already remarked that the nuclei (pigmentary globules) were the parts first formed here. These surround themselves with a cell, which generally goes on enlarging more and more, and is usually polyhedral. Around the nucleus, which looks clear in consequence, and from it outwardly, towards the inner wall of the cell, pigmentary molecules are disposed, whilst the primary walls of the cell continue parted, and, being so, polygonal interspaces are observed between their several layers.—(Vide the choroid coat of the horse's eye). Pigmentary ramifications arise in accordance with the law by which a cell passes into a fibre.—(Vide under VIII. *a*.)

V. *The nuclei surround themselves with extremely delicate cells, and about these a peculiar substance is deposited, which in its capacity of rapid growth soon forms the largest portion of the tissue, and in which, as in all other intercellular masses, new nuclei and cells may be produced.*

Imposed globules of the central and peripheral portions of the nervous system.—The process of development here is best observed in the grey substance of the superficies of the hemispheres. The round granular nuclei, with from one to three generally round, rarely fusiform nucleoli, surround themselves with cells of the utmost delicacy, consisting of a transparent membrane and a limpid included fluid; these, when treated with water, give way and disappear, no trace of them, save their nuclei, remaining; they can actually be seen bursting, the fact being betrayed by the momentary jerk which the nucleus exhibits, the phenomenon being precisely the same as that which Schwann observed in the central substance of young ova (l. c. 57). By and by a substance of a grey or reddish-grey colour, and consisting of fine granules and a transparent uniting mass (a relation which is best seen when a fine slice from an entire—from two to seven inches long—embryo of the cow or sheep, is placed under the microscope without water and by lamp light), arranges itself around this cell. The cells and their burstings are also seen very distinctly, and in precisely the same way, in the granular layer of the retina. The nuclei of the ganglionic globular layers are brighter. In the ganglionic globules the process is analogous to that of the central apposition-globules (*Belegenskugeln*). The reddish-grey matter which is deposited around them is firmer, as it lies more inwardly. In the embryo of the sheep, measuring an inch and three-quarters, all the stages of the development may be seen in the Gasserian ganglion close to one another:—mere nuclei at one part, and at another very minute complete ganglionic globules, evolved at the expense of the external

reddish-grey, finely-granular substance, and which, despite their minuteness, are seen to be round, three-cornered, taper-shaped, and so forth, and generally flattened in a greater or less degree. In the clear nucleus, which is ever relatively the larger as the ganglionic globule is absolutely smaller, from one to three separate nucleoli are contained. On the farther development of the ganglionic globule, vide Müller's *Archiv*, f. 1839.

VI. *The cells exhibit a very high degree of productive or procreative power. New nuclei are perpetually arising within them and there surrounding themselves with cells, we have finally cell within cell, like a nest of pill boxes* (Repertor. i. 34, 175, 286, tab. ii. fig. 35) *; abundance of intercellular substance is at the same time deposited betwixt the parietes of the cells, and these two elements blended together compose the elementary mass,—the cells with their products, the nuclei aud nucleoli, the proper and peculiar corpuscules.* (Schwann, l. c. 26, et sequent.)

Cartilage.—This intercellular substance is more compact; it is granular in the permanent cartilages of the adult, and acquires its higher consistency and its earth in the process of ossification. During this there arise opaque, and by and by ossific reticulations, in the centre of which are seen clearer spaces, often separated by concentric annular striæ, containing cartilage corpuscules with simple or double-imboxed nucleoli. These cartilage-corpuscules pass immediately into bone-corpuscules (*Entwickel.* 263); clear at first, they become more opaque by degrees; they are of large size, push out at one or both points, especially in the first instance, filiform prolongations, which are the first indications of radii, and grow of a darker hue from the periphery towards the centre. When they are still clear but chemically impregnated with lime, their structure is no longer recognizable; if the slice be softened by an acid, however, the nuclei and nucleoli come again into view, in the same way as the numerous smaller bone-corpuscules present themselves in the spongy tissue which surrounds the medullary cavity concentrically, or lengthwise, especially in the bones of adults, and like other cellular fibres contain elongated nuclei with pretty clear, small, and separate granules. On the formation of the medullary cavities, vide *Entwickelungsgeschichte*, 261. In the reticulate cartilage of the ear, the round granular nuclei and the intercellular substance blend together and form a network which hardens and enlarges, and besides the clear cellular substance, contains in its meshes round nuclei, or true cartilage-corpuscules. By reason of the multiplied imboxing in cartilage, the indication of the elements, as cell, nucleus, and nucleolus, is to be viewed as merely relative. On the fibres of the dental substance, which Schwann (l. c. 74), with the greatest probability of being in the right, has referred to this place, my own observations are incomplete. The cells of the primary mass resemble those of the primary substance of the auricular cartilage (in the sheep), and the fasciculate canals seem the analogues of the cellular parietes, or of these and the intercellular substance.

VII. *The cells are tessellated, or spread out into a membrane, in the manner of a piece of pavement; their granular nuclei lie in the middle. The parietes of the cells blend into a transparent simple membrane, whilst the nuclei are ever more and more absorbed; becoming constantly paler, until at length they are no longer recognizable:*

(*a*) Hyaloid membrane; capsule of the lens; elementary membrane of the saccus capsulo-pupillaris.—In the first two of these tissues the nuclei are especially delicate; their extreme paleness soon renders them scarcely visible; by and by, as it appears, they vanish entirely.

(*b*) Inner membrane of the blood-vessels.—In both the arteries and veins of the embryo, as well as in the large vessels of adult animals (the horse), pale granular nuclei are conspicuous. The blending, or fusion of the cells takes place after the fascicular type, which will be immediately described; when detached they therefore usually present themselves as broad cellular fasciculi, evidences of their fibrous structure being readily discovered at every point of the membrana intima. (Müller's *Archiv*, 1838, 196.)

VIII. *The cells and their nuclei arrange themselves in longitudinal lines; the cell-walls coalesce in lines, and, at the cost of the nuclei, form themselves into fibres:*

(*a*) Cellular membrane.—The cells become elongated, coalesce longitudinally, and over and under the nucleus grow smaller, till at length they change into cylindrical fibres. The very delicate cell-paries is produced, or drawn out, over the nucleus, which soon becomes of an elongated round form, but somewhat flattened: in this way arise spindle-shaped bodies containing a granular nucleus, which extend as cylindrical fibres. The arrangement of the individual cell-fibres prefigures exactly that of the future cellular membranous bundles. They form reticulations, the meshes of which are round, and not unlike the cellular tissue of an herbaceous vegetable (*example*, in the connecting tissue of the navel string, and the pulp of a tooth); or they stand in simpler arches (*example*, in the epiploa); or they close in and surround organs and organic parts (*example*, the glands and the several lobules of these); or they are longitudinal (*example*, in the septa of the kidney, the transversely-streaked muscular fibres, upon the blood-vessels, and so forth). In general there proceeds from one of the two ends—and this is that one which is in relation with the nucleus—a simple cylindrical filament of the cell-wall. In the pulp of the teeth it forms with the delicate wall of the cell, a more or less three-cornered central body, from which several, generally three, threads diverge, an arrangement with which Purkinje and Raschkow (l. c. fig. 7) were already familiar. Finally, in the omentum majus of a fœtal calf, nine inches in length, I once observed several cylinders proceeding from the lateral aspects of a spindle of this kind, in addition to the two, one from either end, which are usually encountered. These spindles, with their nuclei, I first noticed in the sheath of the acoustic nerve (*Entwick.* 208). The spindles, with their nuclei, lie at those points where the fibres run longitudinally—straight or concentrically, alternately or severally, whilst the interspaces are occupied by a transparent mass. In reticulate connexions a transparent gelatine lies in the meshes, which in the umbilical cord often contain an isolated granular nucleus, or this included in a round cell. The nuclei are paler, and finally disappear completely, so that instead of a cellulate fibre, a simple fibre is formed, and this separates, in accordance with the laws of separation, into filaments of cellular tissue, which immediately after their acquired individual existence in their free condition, exhibit their elastic undulatory flexions—this is apparent in the sheep's embryo of two inches long. The fibres of the tendons comport themselves in a similar manner, only that here the fibres are thicker, and in the first instance present granular bundles.

(*b*) Elastic tissue.—The cells lie like parenchyma by one another, and are somewhat depressed or flattened, as it seems. Their walls are granular, at the expense of the nuclei, but not so dark as in the horny tissue. By the blending or fusion of these cells arise (in the ligamentum flavum nuchæ) peculiar granular

fibres, which are at the same time covered externally with small molecules. In relation with the parietes of the cells, or as intercellular substance, the elastic fibrous net is now produced, and this, from its thickness, raises and incloses between its meshes the smooth dry granular parietes of the cells—this is apparent in the aorta even of adult animals.

(*c*) Muscular tissue.—So soon as the muscular tissue assumes the fibrous form, it is seen to contain very pale round nuclei, lying in the close vicinity of one another. From this it is fair to conclude, that the cells, in like manner longitudinally arranged, blend together immediately, and without undergoing elongation into filaments. This inference is confirmed by the circumstance that such a muscular fibre in the embryo is seen as a mere succession of chambers, like a fibre of the ova of the confervæ, with its series of cells, and a nucleus in each. I have not hitherto, however, succeeded in obtaining such a view of this multilocular arrangement, as fully to satisfy my mind of its entire and constant accordance with nature. There are two conditions which either bring out the appearance, or render it plainer :—1st. It happens that betwixt each two of the ordinary constrictions of the muscular fibre a regular nucleus is perceived. 2nd. Upon the transverse lines which produce the cancellate divisions, lie very small round molecules, with very dark outlines and transparent centres, in a more or less regularly transverse lineal arrangement. The clear nucleus lies inside the hollow muscular fibre, and is frequently seen projecting, either partially or wholly, from the divided end of the fibre. At a later period it is ever more and more undistinguishable. Longitudinal striæ, and soon after these, transverse striæ, make their appearance in the muscular fibre. That the internal hollow of the muscular fibre remains, is rendered probable by the circumstance noticed by me, now some time ago, to wit, that the ends of the living muscular fibre divided, often become everted (Hecker's *Neue Annalen*, ii. 71). The subsequent stages in the development of the transversely-streaked muscular fibre are treated at length in *Entwickelungsgeschichte*, S. 69.

(*d*) Fibres of the crystalline lens.—That the superficial vesiculate or cellular formation suffers metamorphosis into the fibres of the lens, was shown by me to be extremely probable in 1838 (Ammon's *Zeitschrift*, iii. 330). The cells contain very pale nuclei, with single nucleoli; they then unite longitudinally one with another, like a string of beads, pale nuclei being still discernible inth e cells of most recent formation. Upon the fibres themselves I further observed an extremely delicate granular matter. Each fibre then divides by fine lines into threads, which however cannot be distinctly isolated, even in the adult, and which are remarkable for the beautiful regularity of their arrangement (*Entwick.* 203; Werneck, in Ammon's *Zeitschr.* v. 414).

(*e*) Primary nervous fibre.—The septa arise in the fibres of nerves like those of the muscles, ganglionic globules, and ganglia, glands, &c. out of cellulate fibres, from which the general sheath of a nerve in the first instance, and the special sheaths in the second, become distinguished. Within this sheath we can perceive, but only at a very early period (in the nervus trigeminus and nervus facialis of the sheep's embryo, 1¾ of an inch long, for instance), single primary nervous fibres, which here run as completely isolated as we find them in the pulpy nerves (*in nervis mollibus*) of adult creatures, which are, like these, rendered visible by caustic alkali (when they are not already obvious), and which from the greater relative strength of the sheath first become tortuous after mechanical

traction. The contents are not of a pure white colour, but decidedly yellowish, and the fibre occasionally exhibits a small clear (granular) nucleus in different places of its course. At a later period the fibre becomes white, and the more the sheaths are individualised, the more does it exhibit windings, and increase in breadth and thickness.

IX. Finally, the earthy deposits of the body manifest their cellular relationships in a less obvious manner. The auditory crystals present themselves in the sheep's fœtus of from six to seven inches long, as very small elongated round bodies. If a fine slice of the membranous labyrinth be examined, three or four of these crystals may be seen connected with a nucleus, like so many nucleoli. These minute bodies, even at this early period, when treated with a little nitric acid, give off an abundance of carbonic acid gas. The crystalline globules are laminated, or arranged in layers, around a nucleus (Müller's *Archiv,* 1836, t. x. fig. 13), or around this and a nucleolus (Remak, *Obs. Anat. et Microscop. de system. nervos. struct.* tab. ii. fig. 26; *Repertorium,* iii. tab. i. fig. 6).

From the account now given, it appears that we have an ascending series of formations, in which the types I. II. III. and IV. present perfect analogies with those that are observed in the vegetable world. Types V. and VI. are essentially modified, and appertain to the very highest grades of organic formation. Types VII. and VIII. possess the purely vegetable form only in the very earliest stages; in their perfect conditions they present no analogy whatsoever with any thing we observe in plants, in point of form. The transition stage of the cellular fibre may perhaps be found to present a certain analogy with what Mohl has described and figured in Scytonema myochrus (*Ueber die Verbindung der Pflanzenzellen,* 1835, tab. i. fig. 10), as also in the knotty vessels of the latex of young leaves—in Robinia pseudo-acacia, for example.

The universal primitive form of every tissue is therefore the CELL, which itself is preceded by the NUCLEUS as mediate, and the NUCLEOLUS as immediate products of the formative power. Cells and nuclei seem to stand in mutual and relative opposition, so that generally, perhaps invariably, the one is evolved at the expense of the other. After these transition stadia are accomplished, the tissue attains individuality according to general character and the place it occupies in the system. During this last stage the more distant organic parts enlarge, as is distinctly seen in the cells of the epithelium, in the tubular membrane, in the pigment, the ganglionic globules, the muscular fibres, the tendinous fibres, the primary fibrous fasciculi of the nerves, and the elastic fibres; whilst mere nuclei, such as the blood, lymph, coagulable lymph, and pus-globules remain, or suffer diminution in the course of further development.

That the cellular formation also forms the basis of all the morbid, new, or heterologous formations, is made manifest by the observations of Müller, Henle, and myself. [Vide in particular the work of Müller, *Ueber krankhafte Bildungen, &c.* for an excellent translation of which into English, *On the Nature and Structural Characteristics of Cancer, &c.* we are indebted to Dr. West. 8vo. Lond. 1839. R. W.]

After the above communication of Dr. Valentin was in the printer's hands, I received, through the politeness of Dr. Schwann, a brief notice of the results to which his OBSERVATIONS ON THE DEVELOPMENT OF THE TISSUES had led him; and it affords me

particular pleasure to have the privilege of laying these before my reader in this place.

"All the organic tissues," says Dr. Schwann, "however different they may be, have one common principle of development as their basis, viz. the formation of cells; that is to say, nature never unites molecules immediately into a fibre, a tube, and so forth, but she always in the first instance forms a round cell, or changes, where it is requisite, cells into the various primary tissues as they present themselves in the adult state. The formation of the elementary cells takes place, in the main points, in all the tissues according to the same laws; the farther formation and transformation of the cells is different in the different tissues.

The primary phenomena of the cells are the following: there is first a structureless substance present (cytoblastema), which is either contained in pre-existing cells, or exists on the outside of these. Within this, cell-nuclei generally first arise—round or oval, spherical or flat corpuscles—which usually include one or two small dark points (nuclear-corpuscules). Around these cell-nuclei the cells are produced, and in such wise that they at first surround the nuclei closely. The cells expand by growth, and indeed by intussusception, and the same thing very commonly happens, for a certain period, in regard to the nuclei. When the cells have attained a certain stage of development, the nuclei generally disappear. With reference to the place at which the new cells arise in any tissue, the law is that they constantly appear where the nutritive fluid penetrates the tissue most immediately; therefore it is that the formation of new cells in the unorganized tissues only takes place at the points where they are in contact with the organized matter; in the completely organized tissues, again, where the blood is distributed to the whole of the texture, new cells are produced in the entire thickness of the tissue.

The process, by which the cells evolve themselves into the elementary formations of the individual tissues is very multifarious. The most remarkable differences are the following:—1. The elongation of the cell into a fibre, which probably takes place in consequence of one or more parts of the cell-wall increasing in a greater degree than the others. 2. The division into so many isolated fibres, of a cell elongated in different directions. 3. The blending of several simple or primary cells into one secondary cell.

Cartilage. The cartilages are distinguished among all the tissues of the human body, by containing the largest quantity of cytoblastema, which is also extremely consistent (fig. CXXXIV.) The quantity of cytoblastema, however, differs greatly in different cartilages. It is, for instance, much smaller than usual in the branchial cartilages of the larva of the frog (fig. CXXXV.). Here

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Fig. CXXXIV.

Fig. CXXXIV.—Cartilage; the nidus of the os ileum, but as yet without earthy deposit, from the fœtus of the sow.

the cells may be observed flattening one another as soon as they touch. The first formation, and the subsequent growth of cartilage, take place in such wise, that a cytoblastema is first produced, in which cells then form, whilst at the same time fresh cytoblastema arises, within which again cells are evolved as before, and so the process goes on. As the cartilage is without vessels at first, the formation of new cells only proceeds on the superficies of the substance, or, at all events, in the vicinity of this; in the situation, therefore, where the cartilage is in immediate contact with the nutritive matter. The production and growth of the cells of cartilage are exhibited in figure CXXXV. In the cytoblastema, on the surface of the cartilage at *a*, or between the new-formed cells at *b*, new cell-nuclei are arising. Around these, cells will by and by be formed, as at *c* and *d*, which still surround the nucleus intimately, and are very thin in the walls. These cells expand by growth, and their walls, at the same time, become thicker. The nuclei also grow in a very slight degree for a while. The cells contain now a clear fluid, now a granular precipitate, which generally first forms itself around the nucleus, as at *e*, fig. CXXXV. for example. In the old cells young cells occasionally arise—(Are these fat cells?) By and by cavities or canals (marrow-canals) are formed in the cartilages in a way which has not yet been investigated with sufficient care, through which vessels also take their course. If, after this epoch, any new cells are produced, we may presume that their evolution takes place not only from the surface of the cartilage, but also around these vascular cavities and canals; and, perhaps, it is from this circumstance, that after ossification, the cells are found disposed in laminæ, partly concentric around the cavity of the medullary canal, partly parallel with the surface of the cartilage. In the process of ossification, the earth is first deposited in the cytoblastema of the cartilage. The cells of the cartilage, at the same time, suffer a remarkable change, which seems to consist in this, that they become elongated in different directions into hollow processes or canals, and thus acquire a stellated appearance (stellated cells). The nuclei of the cells, during this process, are absorbed. At length, and finally, the cells themselves, and the canals proceeding from them, appear to become filled with calcareous earth.

Cellular tissue.—The cytoblastema of the cellular tissue is a structureless, gelatinous looking, transparent substance, not unlike the vitreous humour of the eye. Within this arise small round granular-looking cells, furnished with nuclei (fig. CXXXVI. *a*.) Here, too, the nucleus appears to be the part first formed, the cell being developed around it. As the cellular tissue contains blood-vessels, the evolution of new cells also proceeds through the entire substance of the tissue. The cells grow, but scarcely attain to twice the diameter

Fig. CXXXV.

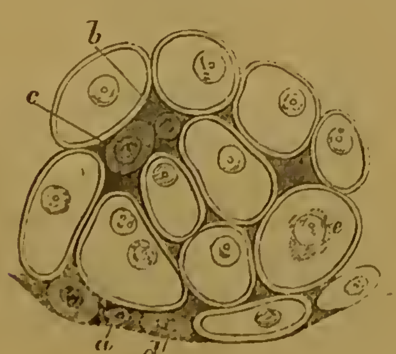

Fig. CXXXV. represents the branchial cartilage of a very young larva of the frog. The lower edge of the preparation is the natural limit of the cartilage.

of the nuclei they enclose; at a very early period, however, they begin to lengthen out in two opposite directions into fibres (fig. CXXXVI. *b*). The fibres then stretch on either hand into several branches (*c*, *d*,) and these, in their turn, proceed, dividing into still smaller fibres. This fibrillation of the branches, however, by and by proceeds backwards, towards the stem of the fibre arising immediately from the body of the cell; so that at a later period, instead of a single fibre, a bundle of isolated fibres is seen proceeding from either side of the body of the cell (fig. CXXXVI. *e*). Finally, the body of the cell itself also splits into fibres, and then, instead of a cell, we have a bundle of particular fibres, to which the nucleus of the former cell still continues attached. This process consists, therefore, in a kind of splitting up of a single cell into a multitude (perhaps of hollow) fibres. At a subsequent period, the nucleus is taken away, so that the fibres alone remain, and compose the filaments of the cellular tissue, as we find them in adults. It would appear, however, that they must suffer a chemical change, in addition to the changes in form, inasmuch as the cellular tissue at first affords no proper gelatine.

Muscle.—The researches of Valentin have shown that the muscles are composed of globules arranged in rows, like strings of beads, which then unite into a fibre,—the primary muscular fibre. The fibre thus evolved is a hollow cylinder, in the cavity of which cell-nuclei lie near to one another (fig. CXXXVII. *a*.) From this it becomes probable, that the globules which compose the fibre were

Fig. CXXXVI.

Fig. CXXXVI. — Various stages in the evolution of the cellular tissue of the fœtus of the sow; the stages are in the order of the letters of reference; *c* and *d* are mere varieties.

Fig. CXXXVII.

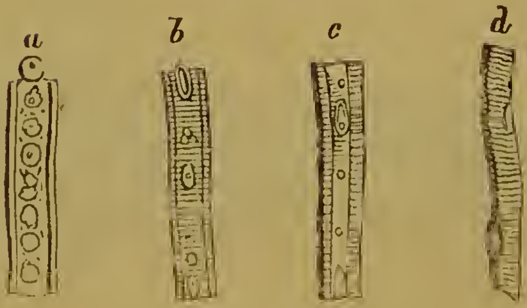

Fig. CXXXVII. *a*, *b*, *c*.—Different stages in the evolution of muscular fibre; *d*, a muscular bundle imperfectly developed, standing on its edge.

hollow,—were cells,—and that the nuclei, included in the cylinder, are the nuclei belonging to these primary cells. The earlier process of evolution, which I have not myself investigated, must therefore have been as follows:—the (hollow) globules or primary cells arranged themselves in a row, or coalesced into a cylinder, and then the septa, by which this cylinder must have been divided, underwent absorption. The nuclei are flat, and lie within the cylinder, not in its axis, but in its walls. This cylinder, rounded and closed at its ends,—this secondary muscular cell, grows continually, like a simple cell, but only in the direction of its length, for it either gains nothing in point of breadth, or it becomes actually thinner. The growth lengthwise, however, does not proceed from the ends only, but through the entire extent of the cylinder, as is obvious, from the fact of the nuclei, which at first lay close to one another, getting more and more distant, and even themselves elongating often in no inconsiderable degree. In this way, the muscular bundle *a*, (fig. CXXXVII.) is changed into the bundle *b*. At this period, the deposition of a new substance upon the inner surface of the parietes of the cylinder, or cellular membrane of the secondary muscular cell takes place, by which its wall is thickened (compare the fibre *c*, with the fibre *b*, fig. CXXXVII.) That the thickening of the wall here is no thickening of the cell-membrane itself, as it is in the case of cartilage, appears from this, that the nuclei are not forced inwards, towards the hollow of the cylinder, but outwards, and continue lying in front of the secondary deposition, as is seen in *d*, (fig. CXXXVII.). The secondary deposition in question goes on until the cylinder is completely filled. The deposited substance changes into very delicate fibres, which run in the direction of the length of the cylinder. These are the primary muscular fibres; together they constitute a bundle, and this is the primary muscular fasciculus, which is inclosed externally by a peculiar structureless wall—the cell-membrane of the secondary muscular cell. A process, in all respect, analogous, occurs according to Meyen, in the cells of the liber, or inner bark of vegetables. Here too, simple cells arise, which arrange themselves in rows, and by coalescing at the points where the cellular parietes are in contact, subsequent absorption of the septa being produced, change into a secondary cell, the wall of which increases in thickness by means of secondary deposition; the only thing wanting in the resemblance is, that this thickening should take place by means of longitudinal filaments.

Nerve.—The nerves appear to be formed after the same manner as the muscles, viz. by the fusion of a number of primary cells arranged in rows

Fig. CXXXVIII.

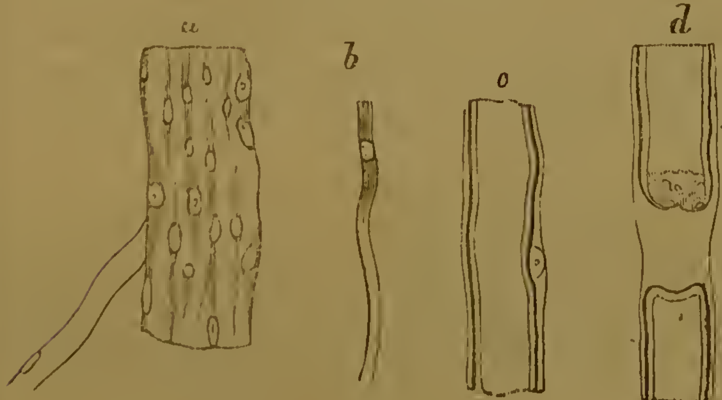

Fig. CXXXVIII.—Different stages in the development of nerve; *a* and *b*, of a very young fœtal sow; *c* and *d*, nervus vagus, from the cranium of a fœtal calf.

into a secondary cell. The primary nervous cell, however, has not yet been seen with perfect precision, by reason of the difficulty of distinguishing nervous cells whilst yet in their primary state, from the indifferent cells out of which entire organs are evolved. When first a nerve can be distinguished as such, it presents itself as a pale cord, with a coarse longitudinal fibrillation, and in this cord a multitude of nuclei are apparent (fig. CXXXVIII. *a*). It is easy to detach individual filaments from a cord of this kind, as the figure just referred to shows, in the interiors of which many nuclei are included, similar to those of the primitive muscular fasciculus, but at a greater distance from one another. The filaments are pale, granulated, and, (as appears by their farther development,) hollow. At this period, as in muscle, a secondary deposit takes place upon the inner aspect of the walls of the fibrils, or upon the inner aspect of the cell-membrane of the secondary nervous cell. This secondary deposit is a fatty white-coloured substance, and it is through this that the nerve acquires its opacity (fig. CXXXVIII. *b*). Superiorly, the fibril is still pale; inferiorly, the deposition of the white substance has occurred, and its effect, in rendering the fibril dark, is obvious. With the advance of the secondary deposit, the fibrils become so thick, that the double outline of their parietes comes into view, and they acquire a tubular appearance (fig. CXXXVIII. *c*). On the occurrence of this secondary deposit, the nuclei of the cells are generally absorbed; yet a few may still be found to remain for some time longer, when they are observed lying outwardly between the deposited substance and the cell-membrane (fig. CXXXVIII. *c*), as in the muscles. The remaining cavity of the secondary nervous cell appears to be filled with a pretty consistent substance, the *band* of Remak, and discovered by him. In the adult a nerve consequently consists, 1st, of an outer pale thin cell-membrane—the membrane of the original constituent cells, which becomes visible, when the white substance is destroyed by degrees, (*ex. gr.* fig. CXXXVIII. *d*); 2nd, of a white fatty substance, deposited on the inner aspect of the cell-membrane, and of greater or less thickness; 3rd, of a substance which is frequently firm or consistent, included within the cells, the *band* of Remak.

Along with these observations, and grounded upon them, Dr. Schwann has communicated to me some general views of the organic powers, which, however, in conformity with the plan of my work, I reserve for another place.

CONCLUDING REMARKS, RETROSPECTIVE AND PROSPECTIVE.

§ 87. After the exposition now given of the various particulars composing the processes of Generation and Development, it would be extremely interesting to trace back the appearances which we have observed to their elements. It cannot, in particular, be

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Fig. CXXXIX.

Fig. CXXXIX.—Cells from the granulations of the umbilical cord of the calf. They bear a striking resemblance to the cellular tissue of vegetables; nuclei are seen included in the several cells. After Breschet and Gluge (*Ann. des Sc. Nat.* t. viii. pl. 6, fig. 5)

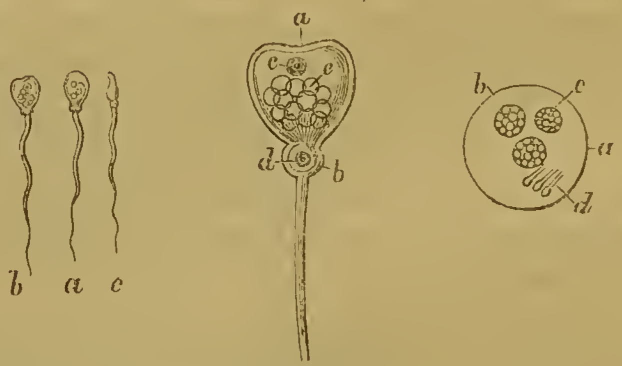
matter of doubt with the considerate observer, that the UNITY OF PLAN which forms the substratum as it were of the vast variety of phenomena occurring throughout creation, must also be cognizable here. The grand features, the chief results, would indeed present themselves simply, and might be announced in few words. But, as no organic process can be comprehended isolatedly in its essence; farther, as that which we in the sequence name with Goëthe, *primary* or *fundamental phenomenon*, cannot be shown from the empirical mode of contemplating an object in itself, but only with the assistance of another cognizant active power, viz. the mind; and finally, as our purpose is to give a THEORY OF ORGANIC LIFE, following from and based upon a careful observation of the elementary phenomena which make up its sum, it is evident that a *general view of generation*, or the THEORY OF GENERATION, can only be in place in our last Book, which comprises the General Physiology. At present, for example, it would be impossible for us, still unacquainted with the process of nutrition, to reduce the genesis of the human embryo to universal laws. A long series of preliminary queries, calculated to shed great light on the essence of the generative process, also requires to be answered; but these, too, upon the plan we have laid down, can only be taken into consideration in the GENERAL PHYSIOLOGY; among the number of queries now alluded to, the following, to select a few, present themselves: to determine the relations of the organism of the parents to the progeny; the hereditary transmission of corporeal forms, of mental aptitudes, and of liabilities to disease; the mode in which monstrosity originates; the numerical relations of the sexes; the resemblance in intimate structure of the objects composing both organic kingdoms, and so forth. These are all obviously subjects for our after consideration [171].

[171] Upon many of the relations just named, see the excellent article GENERATION, of Dr. Allen Thomson, in Todd's Cyclopædia of Anatomy and Physiology, I may be allowed to observe here, that I participate in the greatest degree in the thorough scepticism of the writer upon many points; for example, that the imagination of the mother produces any permanent bodily impression upon the progeny; that transitory states, such as that of intoxication, during the sexual act, can exert any influence on the corporeal or mental development of the being which is its result, &c.; by far the greater number of the data adduced in support of this popular belief will not bear investigation; and others admit of explanations very different from those usually given; it is otherwise, however, with regard to the transmission of the bodily and mental peculiarities which are stamped upon the parents; these, as we shall see at a future period, afford most important strong holds in framing a theory of generation, precisely as a general survey of the realm of organization teaches us to refer the genesis of organic bodies to universal and invariable laws.

[APPENDIX.

Organization of Spermatozoa. Addition to Annot. 13 *et seq. under* § 6.

In the 11th vol. of the *Nov. Act. Acad. C. L. Natur. Curios.* 4to. 1839, there is a paper by G. Valentin on the Spermatozoa of the Bear, in which the question of the organization and consequently of the truly animal nature of the seminal animalcule of this creature seems settled. The accompanying figures and description are copied from the paper.



Spermatozoa of the Bear.

In the left-hand figure, *a,* is the spermatozoon, seen from the upper surface; *b,* from the under surface; *c,* from the side. The middle figure is a view from the under surface of one of the spermatozoa, highly magnified, *a,* the anterior margin bent inwards; *b,* the distinct part of the body situated posteriorly; *c,* thc mouth; *d,* the anus; *e,* the internal vesicles. The right-hand figure is one of the cysts of evolution; *a,* the outer envclope; *b,* the transparent contents; *c,* the vitelli; *d,* spermatozoa already formed.

The writer may be allowed to express doubts of the significance of the markings here set down as *mouth, anus,* &c. This amount of organization seems too much; were it all it is presumed to be here, indications of something of the samc kind would not only be obvious elsewhere, but would probably be quite general.

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END OF PART I.

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THE

SPECIAL HISTORY OF THE VITAL PROCESSES.

BOOK THE SECOND:

OF NUTRITION AND SECRETION.

CONTENTS OF THE SECOND BOOK.

CHAPTER I.

OF THE BLOOD.

CHAPTER II.

OF THE CIRCULATION OF THE BLOOD AND THE VASCULAR SYSTEM.

CHAPTER III.

OF DIGESTION.

CHAPTER IV.

OF RESPIRATION.

CHAPTER V.

OF SECRETION.

CHAPTER VI.

OF ABSORPTION AND THE MORE INTIMATE PROCESSES OF NUTRITION.

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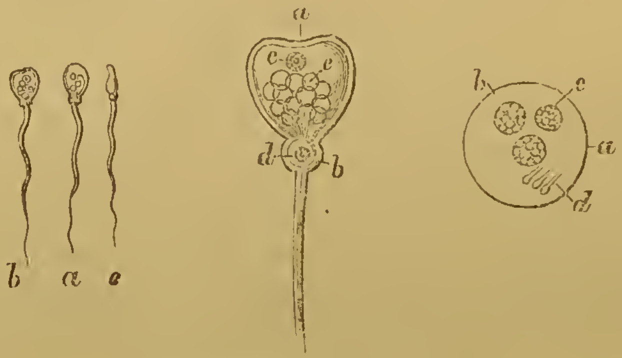

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BOOK THE SECOND.

OF NUTRITION AND SECRETION.

THE SUBJECT AND PLAN OF TREATMENT.

§ 88. So numerous and complex are the systems of organs which concur in the NUTRITION of the animal body, that it is difficult first to separate the processes which belong to these severally, and again to present them united into questionable shapes to the mind. The BLOOD may be assumed as the centre of the entire process of nutrition; it is advisable, therefore, to begin with an exposition of the constituent elements and general properties of the blood. We shall then consider its containing channels, and the manner in which it is distributed to the different parts of the body and is brought into contact with the more delicate organic elements.

The question that first presents itself for consideration is this: how is the blood produced from the food? The answer to which involves an examination of the entire subject of DIGESTION, and at the same time seems to require a glance at the formation of the blood in the embryo. The phenomena of RESPIRATION and SECRETION, again, as processes most intimately connected with sanguification and nutrition, require analysis; they are themselves nearly allied, and their instruments fall under the common head of the vascular capillary system. We shall then pass in review the phenomena of ABSORPTION and NUTRITION in especial, and conclude with a summary of the contents of the present book.[172]

[172] The physiology of nutrition is treated of at great length in the 1st and 2nd Books of Müller's *Physiology*, and in the 4th, 5th, and 6th of Burdach's great work,—*Die Physiologie als Erfahrungswissenschaft, &c.* of which there is a French translation by M. Jourdan, in 9 vols. 8vo.

CHAPTER I.

OF THE BLOOD.

§ 89 *Of the Blood in General.*

THE blood[173] presents itself as a red and warm fluid only in man, mammalia, and birds. In man and mammalia, the temperature of the blood ranges between 97° and 104° F.; in birds it has been found as high as 109° F.[174].

The quantity of blood contained in the body cannot be determined with precision; all the estimates which have been made of the matter are consequently found to differ greatly from one another. Without doubt, the quantity of blood contained in the living body varies to a certain extent with the age, sex, and temperament or constitution of the individual subject examined. It may be stated approximatively at from the fifth to the sixth

[173] A copious index to the very extensive literature of the blood exists in the third volume of Burdach. Among older writings, the most weighty of all are the *Experimental Inquiries* of William Hewson, 8vo, Lond. 1771—1773. The papers of Prevost and Dumas, in the *Bibliothèque Universelle de Genève*, tom. xvii. p. 215 and 294, are also important. So is the contribution of Prof. J. Müller, in Poggendorff's *Annals* for 1832. Among late works, that of Nasse, *The blood in a variety of Relations physiologically and pathologically considered*, (*Das Blut in mehrfacher Beziehung*, *&c.* 8vo. Bonn 1836,) deserves particular mention, [as do our author's *Contributions to the Comparative Physiology of the Blood* (*Beiträge zur vergleichenden Physiologie des Blutes*, 1stes und 2tes Heft. 8vo. Leipz. 1833—1838.) The most original British inquirers, after Hewson, into the Physiology and Anatomy of the blood, are Dr. Davy and Mr. Gulliver. The papers of Dr. Davy, which were hitherto disjecta membra, have been happily gathered together in his excellent work entitled *Researches, Physiological and Anatomical*, 2 vols. 8vo. Lond. 1839. Those of Mr. Gulliver occur in different volumes of the *Lond. and Edinb. Philos. Magazine*, *Proceedings of the Zoological Society*, *Trans. of the Royal Med. and Chirurg. Society*, *&c.* A summary of his views, however, will be found in the Appendix to Gerber's *General Anatomy*, 8vo. Lond. 1842; and in the same place, Tables of the measurements of the blood-discs in upwards of 370 animals. R. W.]

[174] [Although, in comparison with the higher vertebrata, reptiles and fishes may be cold-blooded, yet some of them possess a temperature considerably higher than that of the medium in which they live, and the temperature of one fish at least of the genus Thynnus is nearly or quite as high as that of man. The follow-

of the whole weight of the body, and to amount to from twenty to twenty-five pounds[175]. In Amphibia and Fishes the blood has the red colour of that of mammalia and birds; but its temperature is little if at all higher than that of the surrounding medium. In the invertebrata the crystalline or but slightly tinted chyle which circulates through the vessels is improperly and on ground of analogy only, called blood. Even in the rare instances in which this circulating fluid has a deep red colour, as in the common earthworm and

ing are a few of Dr. Davy's observations on this subject, from his *Researches, Physiological and Anatomical*, vol. i. VIII. and XII.

Name of Animal.	Temp. of Air.	Temp. of Water.	Temp. of Animal.
Testudo Mydas	79.5		84
Common male Frog	60	60	64
Species of Coluber (at Columbo)	81.5		88
Shark	71.5	74.75	77
Bonito (Thynnus Pelamys)	78	80.5	99
Common Trout		56	58

At Columbo, Dr. Davy found the temperature of a large black squirrel as high as 106°, that of a monkey 104½°, and that of a goat 104°. The temperature of sheep in Scotland varied from 101° to 104°, at the Cape of Good Hope from 103° to 104°, and at Ceylon from 104° to 105°. In numerous observations at Chatham, "On the temperature of sheep in winter and summer," the same physiologist observed that the venous blood was often 106° and the arterial 107° and 108°. In London he found the temperature of a common thrush 109°; and that of a pigeon 108°; at Ceylon the temperature of twenty-six domestic fowls in one court varied between 106° and 111°.—*Researches*, vol. i. pp. 182 et seq. and 213 et seq. R. W.]

[175] Valentine has made many experiments on the quantity of blood contained in the bodies of animals; vide *Repertor.* B. III., 1838. p. 281. In dogs, from which the most certain inferences may be drawn, he found that the weight of blood relatively to that of the body was in the mean as 1 is to 4,50; in man he estimates the ratio to be nearly as 1 is to 4,25; for it appears from his experiments that the greater the weight of the body of a species or of a genus, the greater also is the relative quantity of blood. Estimates of older date of the quantity of the blood may be found in Haller, *Elementa Physiologiæ*, tom. ii. p. 1, et seq., and in Herbst, *Com. hist. critica, &c. de Sanguinis quantitate*, Götting. 1822. The majority of estimates lie between 15 and 30 pounds; some few, however, speak of no more than 8 pounds; some, on the contrary, are in favour of as many as 100 pounds of blood!

the leech, it does not deserve the name of blood. In the vertebrata the blood is inclosed in tubular and closed but mutually communicating canals, in which and by means of which it is conveyed to all parts of the body. Two principal kinds of blood are distinguished: *arterial blood*, which has a brighter colour; which, received by the heart from the organs of respiration, is sent to the extreme peripheral parts of the body through the arteries; and *venous blood*, which is of a deeper or blacker hue, and from the periphery of the body flows back through the veins to the heart, from whence it is conveyed to the respiratory system, again to be changed into arterial blood and fitted for re-transmission by the arteries to all parts of the body. In the mechanical arrangement of its constituents, as also in its physical and chemical, and in its living properties, the blood exhibits highly complex relations, as the following analytical mode of regarding it will make apparent.

§ 90. *Microscopic Analysis of the Blood. The Blood-Corpuscles.*

The microscopic study of the blood, which ought to precede analysis of every other kind, and without which those that are physical and chemical in their nature have no sure foundation, has occupied the attention of a host of the older as well as of the later observers; there is perhaps no limited portion in the whole domain of physiology that is the subject of such numerous and minute observations as the blood. In examining the blood microscopically, many precautions are indispensable, no other organic fluid being so readily altered by external agencies. The blood that is examined, for instance, must be quite recent, and is best obtained from a puncture or scratch of the skin, and diluted with a small quantity of albumen or serum; the fresh-drawn whipt blood of a venesection may also be used with propriety. A magnifying power of from three to four hundred is necessary to obtain good views.

If no change has taken place in the minute drop of blood examined, it is found to consist almost entirely of a multitude of small rounded bodies, the *blood-corpuscles*, or *blood-discs* [176], swimming

[176] Malpighi was the original discoverer of the blood-discs; Leeuwenhoeck described them more particularly, and named those of the human subject *globuli sanguinis;* those of other vertebrate animals he spoke of under the title of *particulæ sanguinis*. Fontana mentions them generally as the *particulæ sanguinis;*

in a comparatively small quantity of limpid and colourless, or slightly yellowish coloured fluid, the *liquor sanguinis* or *plasma.* This fluid is seen forming a narrow border about the drop of blood; alcohol added to the drop precipitates the albumen contained in it in the shape of a granular matter, intermingled with the blood-globules, and so renders its existence also microscopically apparent. In the recent state the plasma or liquor sanguinis is a perfectly homogeneous fluid. The blood-globules in man appear distinctly discoidal (Fig. CXL, A.), and vary between the 300th and the 400th of a line in diameter; they are rarely seen either larger or smaller. That they are flat disc-like bodies is discovered by examining them on different sides. At the beginning of an observation, before the drop has spread itself abroad completely and the globules have come to rest, or at any time when the port-object is inclined a little one way or another, numbers of them are always seen on their edges (A. *b.*), when they appear as long shaped bodies bounded by two parallel lines. They are also seen falling or rolling over (*), and with every thing at rest finally sinking down upon their flat sides. (*a*). The blood-discs are severally so pale in colour and so transparent, that when one lies over another, the undermost is

Hewson, Rudolphi, and Schultz style them blood-vesicles—*vesiculæ sanguinis;* Doellinger preferred the name blood-granules—*granulæ sanguinis*, and Müller that of blood-corpuscles—*corpuscula sanguinis*, and this last is probably that which, under all the circumstances, is the most universally applicable, and therefore the best.

Fig. CXL.

Fig. CXL.—Globules of the blood of the human subject, the blood having been drawn from a vein and beaten to separate the fibrine. A, Blood globules, seen, *a*, on the flat aspect; *b*, standing on the edge; *, three-quarter view. B, A congeries of blood-globules, with their flat surfaces in opposition, and forming columns such as are made by a number of coins laid one upon another. C, A blood-globule in process of alteration, such as simple exposure to the air will produce. D, A lymph-globule, mingled with the proper blood-globules.

N. B. The subjects of this and the succeeding figures of blood-discs from the *Icones Physiologicæ*, are all magnified to the same extent, viz. about 900 diameters.

seen distinctly shining through the uppermost (*a* inferiorly). If quite normal, a delicate semicircular shadow upon the flat surface gives the observer the idea that the blood-discs are very slightly hollowed out or sunk in the manner of a concave lens. In a short time, sometimes after the lapse of a few seconds only, particularly when the diluting medium has not been well selected, though it also happens from the action of the air, the blood-discs begin to suffer change; they appear puckered and uneven, they acquire notched edges and are stellated, they seem to be made up of very minute globules, or they look like mulberries or raspberries (C). The blood-discs seem to have a natural tendency to approximate by their flat surfaces, and go to form columns such as are produced by pieces of money piled one upon another (B.)[177]

§ 91. It is a matter of interest to compare the blood-corpuscles of the lower animals with those of man. In the mammalia they are in all essential respects the same as in man, round and discoidal; for the most part, however, particularly among the ruminants, decidedly smaller (fig. CXLI.); in the monkeys, again, they are very nearly of the same size.[178] In birds, on the other hand,

[177] On this point see my *Contributions to the Physiology of the Blood*, (*Beiträge zur vergleichenden Physiologie des Blutes*, Heft. ii. S. 6.) I have observed these columns to be formed with great constancy in the switched blood of individuals bled on account of inflammation; they also occur, however, in the blood of persons in perfect health. See farther Ascherson's observations in Müller's *Archiv*, 1837, S. 458. He imagines that there is always some fibrine left in the most carefully whipt blood, which serves as the bond between the blood-corpuscles. The literature of the blood-corpuscles, and the various methods that have been employed to observe them, to measure them, &c., may be found in Weber's edition of Hildebrandt's *Anatomie*, B. i., S. 146.

[178] The blood-corpuscles of the Monkeys are in no wise to be distinguished from those of man. In different human subjects,—men, women, children, negroes, I could perceive no difference. [" The monkeys both of the old and new continent have corpuscles differing but little from those of man," says Mr. Gulliver, vide his interesting "*Observations on the blood-corpuscles of mammiferous animals*," in Appendix to Gerber's *General Anatomy*, *Lond.* 1842. In the marsupial animals it is interesting to know that the blood-corpuscles are nearly allied in form and size to those of the corresponding placental Mammalia as first noticed by Mr. Gulliver. (Vide *Dublin Med. Press*, Nov. 1839, and *Lond and Edinb. Philos. Mag.* Dec. 1839.) In the article MARSUPIALIA, *Cyclop. of Anat. and Physiolog.* Nov. 1841, Mr. Owen refers to a paper of his in connexion with this point, in which, however, there must be a mistake, as I do not find the name of any marsupial animal mentioned. R. W.]

the blood-corpuscles are very different, having an elongated oval shape (fig. CXLII. *a*), and their broad sides instead of being depressed are vaulted or raised (*b*); they are on an average from $\frac{1}{125}$th to $\frac{1}{150}$th of a line in length and about half as broad.[179] It is among Amphibia that we meet with the largest blood-corpuscles; they are

[179] It is very remarkable that in Birds, a class of animals so similarly organized, the blood-corpuscles should appear to present no differences either in respect of form or size in the several orders. [That this statement is too general has been proved by Mr. Gulliver's very curious and minute observations. He found that the size of the blood-corpuscles in birds generally bore even a closer relation to species than in mammals. In the Condor Vulture, for example, the mean long diameter of the blood-discs was $\frac{1}{1761}$st, the mean short diameter $\frac{1}{3392}$nd of an E. inch; some of the discs measuring as much as $\frac{1}{1525}$th of an E. inch in length, and $\frac{1}{3000}$th in breadth. In the common wren, on the contrary, the mean long diameter of the blood-discs did not exceed $\frac{1}{2359}$th of an E. in. and their mean short diameter $\frac{1}{4133}$rd of the same scale. It may also be stated here, after the same writer's researches, that in mammals the blood-corpuscles differ remarkably in size, even in nearly allied families of the same order. There is a wide difference, for instance, between the discs of the smallest and largest ruminants; and the Canidæ have much larger discs than the Viverridæ. In the same way, the snowy owl, as well as some other birds, and even reptiles, have longer and narrower corpuscles than their congeners.—(Gerber's *Anat.* Appendix.) R. W.]

Fig. CXLI.

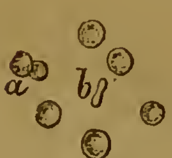


Fig. CXLI.—Blood-globules of the common goat, (Capra domestica.)

Fig. CXLII.

Fig. CXLII.—A, Blood and lymph globules of the pigeon, (Columba domestica). B, A blood-globule, treated with diluted acetic acid; C, with water, by which the central nucleus becomes visible.

here, as in birds, oval-shaped, but relatively somewhat broader, and their surface is rather depressed than vaulted. They are particularly large in the naked amphibia; in the Proteus, for example, they are from $\frac{1}{30}$th to $\frac{1}{50}$th of a line in the long diameter, and are even distinguishable as little points by the naked eye (fig. CXLIII. *a*, *b*); they are consequently from eight to ten times larger here than in man.[180] After the Proteus we observe the largest blood-corpuscles in the land salamanders, where they measure in the long diameter from the $\frac{1}{50}$th to the $\frac{1}{60}$th of a line. In the water salamanders they are still very large—from the $\frac{1}{70}$th to the $\frac{1}{80}$th of a line in length (fig. CXLIV.); in the frog and toad they are from the $\frac{1}{80}$th to the $\frac{1}{100}$th of

[180] [In the Siren, Mr. Gulliver found the average length of the dises $\frac{1}{435}$th, and the breadth $\frac{1}{800}$th of an E. ineh; the nuclei were $\frac{1}{1142}$nd of an E. inch long, and $\frac{1}{2700}$th of an E. ineh broad. *Gerber's Anat.* App. p. 52. R. W.]

It is particularly remarkable that the blood-corpuscles of amphibia present differences in relation with the general zoological position of the several orders: the sealy amphibia, lizards, serpents, and tortoises, are distinguished very remarkably in their general organization and mode of development from the naked amphibia, whieh, like the several families and speeies of the entire order, present great differenees in their structure at large, and also in the sizes of their blood-corpuseles.

Fig. CXLIII.

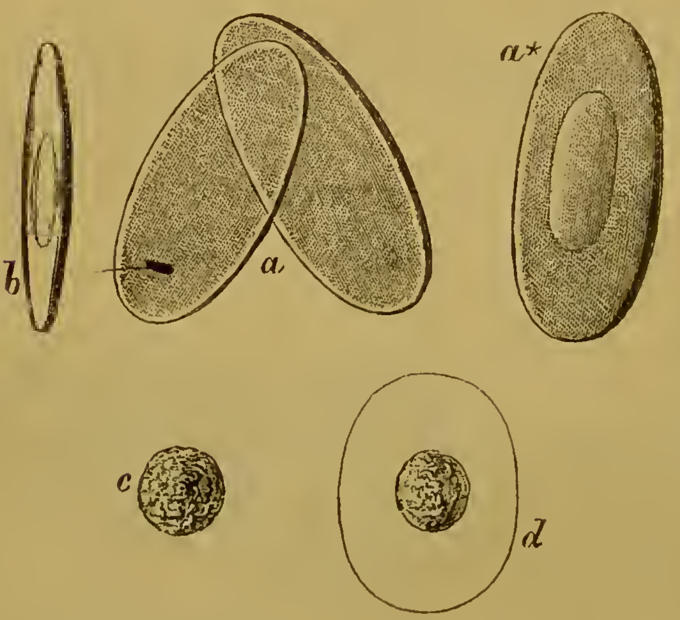


Fig. CXLIII.—Blood-globules of the Proteus anguineus. In the globule *a** the nucleus is seen, and in the globule *d*, which has been treated with water, it is still more apparent; *c*, is a lymph-granule.

a line in length (fig. CXLV.) In the lizards, serpents, and tortoises, they are throughout smaller, though still measuring from the $\frac{1}{122}$nd to the $\frac{1}{150}$th of a line in length[181].

[181] See my *Contributions*, &c. (Beiträge, &c. i. and ii.) A remarkable exception, if the observation be confirmed, occurs in the blood-corpuscles of the camel, which Mandl has described and figured (*Anat. Micros.* pl. ii. fig. 4) as of an oval figure.

[Dr. Mandl's observations have been amply confirmed and extended by Mr. Gulliver (*Med. Chir. Trans.* v. 23, p. 23) ; the mean long diameter of the blood-corpuscle of the dromedary he found to be the $\frac{1}{3254}$th of an E. inch ; and the mean short diameter the $\frac{1}{5921}$st of the same standard. In the Paco (Auchenia paco) and Guanaco (Auchenia glama) the blood-corpuscles scarcely differed in form and size from those of the Dromedary; but in the Vicugna they were slightly smaller, their average long and short diameter being respectively $\frac{1}{3555}$th and $\frac{1}{6444}$th of an E. inch. In structure and magnitude, however, these oval blood-corpuscles of the Camelidæ belong entirely to the mammiferous type ; they have no nuclei like those of birds, and the discs are not much more than half the size of even the smallest that have been observed either in birds or reptiles. The blood-corpuscles of Mammals, it is also to be understood, differ widely in many instances from those of man in point of magnitude. The average diameter

Fig. CXLIV.

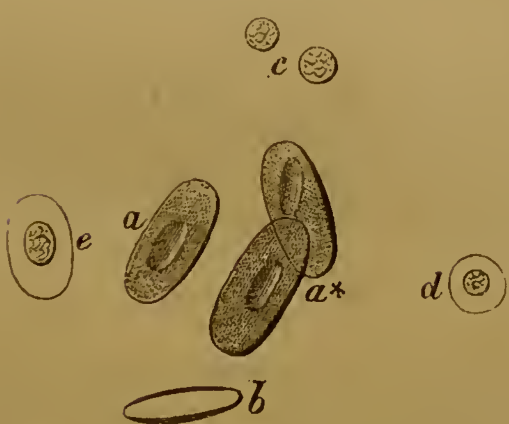
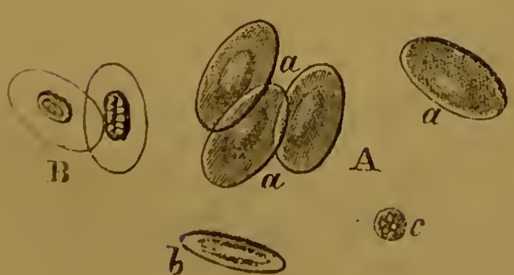


Fig. CXLIV.—Blood and lymph-globules of the great water-newt (Triton cristatus). *a*, *b*, Blood-globules. *a** A blood-globule with excentric nucleus; *c*, lymph-granules, *d*, *e*, blood-globules in progress of development; they are surrounded with delicate involucra. Globules of this description are found abundantly in the blood of well-fed animals generally.

Fig. CXLV.



A. *a*, *a*, *a*, *b*, Blood-globules of the edible frog (Rana esculenta;) *c*, lymph-granule. B, Blood-globules after the action of acetic acid.

In the majority of fishes, and particularly in all the bony fishes, the blood-corpuscles are of a rounded oval (fig. CXLVI), not much longer than broad, flattened, and from the $\frac{1}{150}$th to the $\frac{1}{200}$th of a line in the long diameter; in the skates and sharks, again, they are notably larger, and very similar to those of the frog; they are as much as from the $\frac{1}{50}$th to the $\frac{1}{100}$th of a line in the long axis. It is remarkable that in the Cyclostomes they greatly resemble those of man, being rounded, discoidal, vaulted, slightly biconcave (fig. CXLVII. *a, b*), and measuring $\frac{1}{200}$th of a line in diameter. They are, therefore, only somewhat larger than in man[182].

In the invertebral series of animals they are generally irregular, granular, rounded corpuscles[183].

of those of man, according to Mr. Gulliver, is the $\frac{1}{3300}$th of an E. inch; but the average diameter of those of the elephant, according to the same observer, is as much as the $\frac{1}{2745}$ths of an E. inch, which were the largest he observed among the mammalia. The corpuscles of the Napu Musk Deer, (Moschus Javanicus, Pallas) on the contrary, were no more than the $\frac{1}{12325}$th of an E. inch, some of the corpuscles being actually so small as the $\frac{1}{16000}$th of an E. inch in diameter. From a comparison of the blood-corpuscles of animals of different orders, it has hitherto been supposed that there is no relation between the size of the animal and that of the corpuscles; but Mr. Gulliver has shown that the larger species of the same family of birds and mammals have generally larger blood-corpuscles than the smaller species. See Gerber's *General Anatomy*, App. p. 4, 42 and 44. R. W.]

[182] In fishes the same law still obtains: the form and size of the blood-corpuscles are in relation to differences in the rest of the organization.

[183] Figures of the blood-corpuscles of Invertebrata will be found in my *Contributions* (H. i. fig. 8, 9, 10, 11 and 12), in Mandl's *Anat. Micros.* i. ii. and in Ehrenberg, *On the Structure of the Organ of the Soul (Ueber die Struktur des Seelen-Organs*, Tab. vii. Berl. 1836.)

FIG. CXLVI.

Fig. CXLVI.—Blood and lymph-globules of the loach, (Cobitis fossilis); *a*, *a*, *b*, perfect blood-globules; *d*, blood-globule altered by the action of water, and showing its nucleus; *c*, lymph-granules.

FIG. CXLVII.

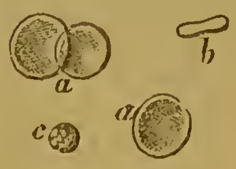


Fig. CXLVII.—Blood-globules of the Ammocœtes branchialis; *a*, *a*, *b*, perfect blood-globules; *c*, lymph-globule. The blood-globules are exactly similar in the lamprey, (Petromyzon), and unlike those of all other fishes, whether cartilaginous or bony.

§ 92. For the study of the structure, vital properties, and chemical constitution of the blood-corpuscles, it is advisable to begin with those of the frog or water-newt, which are almost everywhere to be had easily and at all times. The blood-corpuscles of man and the mammalia are too small to be well adapted to such inquiries. In the blood-corpuscles of the frog (fig. CXLV. A. *a*, *b*), particularly when the blood is not quite fresh, a central oval spot is perceived, which looks like an included nucleus (*b*). If a very small quantity of water, or better of vinegar or acetic acid, be added to the drop of blood under examination, this nucleus is seen to become disengaged and to present itself as a well-defined, dark, elongated and somewhat puckered body (B), which occasionally also appears excentric (fig. CXLIV. *a**). The other portion of the blood-corpuscle has meantime become much paler (fig. CXLV. B). In this way, we discover that the blood-corpuscle [of the frog] resolves itself distinctly into a kernel,—*nucleus*, and a cyst or envelope,—*legumen*, and consequently has the perfect constitution of a cell, as this elementary structure presents itself to us, forming the basis of almost all the solid parts of animal and vegetable tissues. Whether or not the two elements now indicated co-exist in the living blood,—in the blood included within the vessels of a living animal, it is difficult to determine. It is true that we do sometimes see the nuclei of corpuscles which are still circulating through the vessels of transparent parts; but as a general rule this is not the case, or if we think that we perceive them it is very indistinctly (vide figs to § 121 et seq.) In man and the mammalia, we occasionally also succeed in bringing into view a very small nucleus by the treatment indicated; but this is never so constant, and frequently nothing of the kind can be seen; it is, therefore, very doubtful whether the blood-corpuscles of man and the mammalia have any central part corresponding to the nucleus of those of amphibia [184].

[184] The existence of a nucleus in the human blood-corpuscle, which at a former period seemed to me probable, has lately again become doubtful. Müller, Krause, and others admit nuclei. The latter says, "The granules that remain after blood has been treated for a couple of days with distilled water (nuclei of the blood-granules), are $\frac{1}{1204}$th of a line in diameter, but are much more difficult to be seen than many other parts of far smaller dimensions, from refracting transmitted light but very slightly (Müller's *Archiv*, 1837. S. 4.)

[The most careful English observers seem agreed that in the blood-corpuscles of man and the mammalia, there is no central nucleus resembling that of birds, reptiles, and fishes, where it is always very distinct, its existence being demon-

§ 93. Common soft or distilled water reacts powerfully upon the blood-corpuscles. If we add a little distilled water to a parcel of

strated with the greatest ease. The particles that remain after human blood has been treated with distilled water, are the blood-corpuscles themselves, somewhat reduced in size, from having lost all their colouring matter, and having no resemblance, even when made more distinct by corrosive sublimate, to the nuclei of the corpuscles of the lower vertebrate animals. As to the minute granules seen by Krause, it should be recollected that particles of similar size are contained in the blood, and that they are abundant in various animal fluids. See *Gerber's Anatomy*, App. pp. 23. 94. and 103. R. W.]

[By the action of water or acetic acid, the nuclei of the blood-corpuscles of the oviparous vertebrata are instantly exposed in the clearest manner, thick, oval, or spherical; and, as is usual with nuclei of cells, very much smaller than their envelopes. The nuclei of the corpuscles of birds and reptiles may also be shown very easily merely by breathing slightly on some blood dried on glass, which can

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Fig. CXLVIII.

A

Fig. CXLVIII. A In the upper half of the engraving are shown the membranous bases of the human blood-discs, forming a great part of the colourless residue after repeated ablutions of the corpuscles with water. In the lower part of the figure are seen five entire corpuscles as they appeared before washing.

B

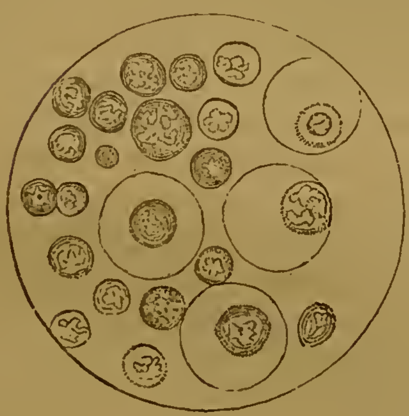
B Blood-corpuscles of the fœtal kitten mentioned above. In the upper part of the figure, are a few corpuscles no larger than those of the mother; to the left are three naked nuclei, and to the right is one larger colourless globule.

the blood-corpuscles of a frog, contained in a watch-glass, they may be seen under the microscope to swell up, and rapidly to be-

be again quickly dried and preserved for future demonstration. Now when the blood of a mammal is treated by any of the means just mentioned, no disclosure whatever of similar nuclei results. But it has long been known that, though the colouring matter is removed by water or acids, the human blood-corpuscle is not dissolved by these reagents. Schultz, in particular, adduces experiments conclusive in this respect, and Dr. Hodgkin and Mr. Lister allude generally to the same fact as regards the action of water. After the colouring matter has been entirely removed by water, the base of the disc remains; it is flat, pellucid, almost as large as the entire corpuscle, and with a refracting power so like that of water as often to require the addition of corrosive sublimate to render the object distinct. In some human blood-discs which, before washing with water, had an average diameter of $\frac{1}{3429}$th of an E. inch, I found the remaining membranous bases $\frac{1}{4800}$th of an inch (see *Phil. Mag.* Feb. 1840, p. 106—7), and this

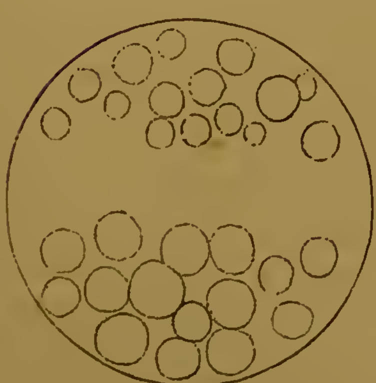
Fig. CXLVIII.

C



C The same corpuscles treated with acid. Numerous pale spherical nuclei are shown detached, and others are still surrounded by faint envelopes. Some of the nuclei appear to contain nucleoli.

D



D Outlines of blood corpuscles from the maternal part of the placenta and from the vena cava of the cat, from which the fœtus spoken of above was taken. In the upper part of the figure are shown the discs from the placenta, which in this instance are rather smaller than those depicted in the lower half of the figure from the vena cava. The blood-corpuscles in the vessels going from the placenta to the umbilical cord, were like the corpuscles from the fœtus shown in B.

The objects in the four circles, comprised under this figure, are all magnified about 840 diameters. G. G.

come round and globular. If the glass with its contents be placed carefully in the midst of a large quantity of water, and be examined after it has stood for twenty-four hours or more in cool weather, the colouring matter will be found to have been completely dissolved out. In the glass itself, we find a white precipitate, which, under the microscope, appears to be entirely composed of the nuclei of the blood-corpuscles; these are therefore insoluble in water and now appear colourless. With a good light, however, the colourless capsules or envelopes of the corpuscles can still be dis-

agrees very nearly with the observations of Sir E. Home, who represents twenty-five of the corpuscles without colouring matter as occupying the same spacc as sixteen of the perfect corpuscles (*Phil. Trans.* 1818, p. 194—5. pl. 8. figs. 1, 2, and 3.) If this ecntral mcmbranous base be called a nucleus, of course the blood-discs of mammals must be said to contain one; but then it must be added that this so-called nucleus has no resemblance to that of birds, reptiles, or fishcs, either absolutely or rclatively to the entire corpuscle.

But in the earliest period of the formation of the corpuscles in the mammiferous embryo, although they are circular in figure, yet in structure and size they completely resemble those of the lower animals; as would appear from the following observations. In fœtal kittens, about half an inch long, I found the corpuscles very variable in size, the majority of them $\frac{1}{2233}$rd of an E. inch in diameter, or about twice as large as those of the mother. These large fœtal corpuscles had a lenticular appearance, by no mcans biconeave; they were of a dcep red colour, but more transparent than in the adult, and nuclei could be distinguished in the centre of somc, and towards the edges of others. A little dilute acid immediately rendcred these nuclei perfectly distinct, so that they were seen to be globular, finely granulated, pallid, and about $\frac{1}{4500}$th of an E. inch in diameter; a few of them exhibited an appearance of nucleoli, and the nuclei were altogether much like lymph-globules. It is probable that the nucleus of the blood-corpuscle of the mammiferous embryo is the true analogue of the nucleus of the blood-corpuscle of thc oviparous vertebrate animal; but in the latter the nucleus is pcrmanent, while in the former it disappears at an early period of intra-uterine life.

In some birds, as the common fowl, the length of the nucleus of the blood-corpuscle is not much greater than its breadth; but in most birds the nuclcus is a more elongatcd ellipse than the envelope. Assuming the breadth of the nucleus as 1, its length would be from $2\frac{1}{2}$ to 3, while the long diametcr of the envelope would scarcely be twice its short diameter. In many fishes, on the othcr hand, the nuclei of the corpuscles are but slightly oval, often ncarly or completcly eircular, as indeed are the envelopes. The envelopes of the blood-corpusclcs in fishes are prone to change much more quickly than the samc parts in birds and reptiles. In many fishes, so fugitive are thc envclopcs, that in a very fcw hours thcy will entircly disappcar, so that when a drop of their blood is subjected to the microscopc, nothing but a congerics of the littlc nuclci is to be sccn. Thesc facts may be easily observed in the blood of the common tench. G. G.]

covered; they are not actually dissolved, but with care may be seen still surrounding the nuclei like rims or frames at a litt'e distance, and only rather smaller than they were at first. The same appearance may be produced in a much shorter time by the agency of vinegar or dilute acetic acid ; but then the nuclei appear of a pale red colour. If to the corpuscles in this state a little strong tincture of iodine be added, the envelopes immediately appear quite distinctly and of an intense brownish yellow hue[185]. The nuclei are neither soluble in water nor in acids; but readily so in alkalis[186].

From these particulars it appears that the colouring matter of the blood is principally contained in the capsules of the corpuscles; that these capsules are extremely delicate membraniform structures, which are impregnated with the colouring matter, and are thereby rendered tumid, and that the nuclei have a structure and chemical qualities different from the capsules[187].

§ 94. The capsule of the blood-corpuscle is highly elastic; the large blood-corpuscles of the frog, and still more readily those of the water-newt, can be pressed flat and extended on all sides between the nicely polished glass plates of the compressor, but on the pressure being removed, they immediately return to their pristine form and size.

185 This interesting fact was first observed by Schultz, loc. cit. p. 18. Other reagents were tried by Müller *(Physiology)*, and by Schultz, but they led to no conclusions different from those stated.

[Mr. Gulliver prefers a strong solution of corrosive sublimate to any other reagent. It is very powerful in bringing into view all the parts of the blood-corpuscles which have become transparent under the action of water, either by rendering them opaque, or by altering the refracting power of the surrounding medium. R. W.]

186 The blood of frogs is best obtained by collecting it from the heart of one or more of these animals in a narrow test glass. The fluid is then to be stirred with a fine glass rod, by which the fibrine will be coagulated and made to fall in flocks, or to attach itself to the rod in the form of a membrane. The blood-corpuscles soon sink to the bottom through the serum, which then presents itself as a yellowish fluid. The blood can be preserved in this state for several days in cool weather.

187 It is not quite determined whether the colouring matter is contained in the capsule of the blood-corpuscle only, or in its central nucleus (when it has one) also, this being itself by possibility a product of chemical agency, for we have no means but those indicated of exhibiting it isolatedly.

The elasticity of the blood-corpuscles can be still better and more strikingly seen by putting the lung of a frog or newt into the compressor. As the screw is turned, the blood-corpuscles are seen flowing through the capillaries towards the side of least pressure, and endeavouring to escape; here they are observed heaped together, and forced into all manner of shapes, some of them pointed, others pyriform, others fiddle-shaped, and these different forms assumed by each in succession as it passes along; as soon as the pressure is taken off, however, all of them immediately recover their appropriate shapes. In the course of this experiment, the blood-corpuscles are discovered to be completely smooth on their external surface,—they seem to glide or slip over one another without showing the slightest disposition to cohere, or to obstruct each other. When the blood-corpuscles have water added to them, the capsules give way and the nuclei float about at liberty. Sometimes, too, the capsules appear plicated and bent in[188].

§ 95. *Lymph-corpuscles,—the second form of solid element of the blood.*

Besides the red coloured corpuscles now described,—the proper blood-corpuscles,—there are other colourless corpuscles contained in variable numbers, but always in relatively small proportion, in the blood of all vertebrate creatures, man among the number. These corpuscles in Fishes, Amphibia, and Birds, are readily recognized from their smaller size and their peculiar appearance. They are very similar in all the lower animals, and measure from the

[188] This peculiar elasticity of the blood-corpuscles was known to Leeuwenhoeck and others, his contemporaries. [It is displayed without the aid of any artificial means: in those capillaries of the web of the frog's foot through which the blood-corpuscles flow in single files, they may always be observed assuming such variety of shapes, as enables them to accommodate themselves to the canal they are traversing, and to their mutual pressure, and forthwith resuming their characteristic forms when they escape into vessels of larger calibre. Mr. Gulliver has given a figure of some peculiar forms, chiefly stellated and crescentic, which the blood-discs of mammals, especially those of certain deer, occasionally assume. Although the forms in question may not be permanent, it is certain that they were observed a few minutes after the blood was drawn, and that they remained with their singular shapes for some days. See *Phil. Mag.* for Nov. 1840, and App. to Gerber's *Anat.* p. 10 and 11. R. W.]

$\frac{1}{200}$th to the $\frac{1}{400}$th of a line in diameter, though many may be found that fall short of this estimate, and others that exceed it; they are colourless, but as they refract the light strongly, they appear with dark contours; they have generally a rounded figure, though sometimes they are long shaped and present a granular appearance (figs. CXLII. et seq. *c*)[189]. These corpuscles are more difficult of discovery in the blood of man and the mammalia, and indeed are apt to be entirely overlooked; for here they occur not only as large as the proper blood-corpuscles, but often larger and often smaller also than these; still their granular appearance, their peculiar contour, and the irregular shading of their surface, the result of irregularity of figure, enable us with a little attention to distinguish them here. (fig. CXL. D; CL. *c*)[190]. They are also remarkably distinguished from the true blood-corpuscles by the different way in which they are affected by reagents. They are not attacked by water, but remain in it for a long time without apparent change; they are not rendered transparent and dissolved by acetic acid; they only become more decidedly granular under its action, and a kind of nucleus is developed in their centre. Caustic alkalis dissolve them at once. They are always found most plentifully in well-fed animals; in such as have fasted for a long time they are much rarer[191]. As these bodies are in all respects like those of the lymph and chyle, and as they have the same chemical relations as

[189] They are of different sizes, though this is within very narrow limits, in different animals, and in respect of size, stand in relation to the proper blood-corpuscles; they are consequently largest in animals that have the largest blood-corpuscles, viz. the naked amphibia and the true cartilaginous fishes. See my *Contributions*, &c. ii. p. 21.

[190] It is very necessary to guard against confounding the lymph-corpuscles now described with the altered blood-corpuscles already indicated and depicted in figure CXL. C., with which the representation of the true lymph-corpuscle, D., may be compared. The difference in colour and in the whole appearance of the two kinds of corpuscle will with the slightest attention prevent any mistake. In nature the dissimilarities are much more striking than they appear in the figure.

[[191] In his *Contributions*, &c. ii. p. 22, Dr. Wagner says: "the number of lymph-corpuscles was always found remarkably great in well fed frogs just caught in the summer season; on the contrary they were very scanty in those that had been kept long without food and in those examined during the winter." In two series of experiments undertaken in August 1836 and February 1837, the following results were obtained:

these, they have very naturally been regarded by many observers as the corpuscles of the lymph mingled with the blood, and designated accordingly *lymph-corpuscles* [192]; but others have viewed them as globules of coagulated fibrine [193], and yet others, as blood-corpuscles in progress of solution or disintegration. These peculiar corpuscles are seen in the capillary system of living animals swimming amidst the proper blood-discs, but more constantly apart as it were from the great stream, and moving in the slower current that is in immediate contact with the parietes of the vessels. They are not elastic like the blood-corpuscles, and seem to stick more readily to one another. They present great similarity in form and chemical relationships to the blood-corpuscles of the inverte-

Experiments of August 1836.

1.	In a field comprising	58	blood-discs, there were found	9	lymph-corpuscles.
2.	— —	54	— —	10	—
3.	— —	74	— —	12	—
		186		31	

The lymph were to the blood-corpuscles in the proportion therefore of 1 to 6 exactly.

Experiments of February 1837.

1.	Among	28	blood-corpuscles, there were	2	lymph-corpuscles.
2.	—	40	— —	2	—
3.	—	30	— —	3	—
4.	—	44	— —	2	—
		142		9	

Here consequently the lymph were to the blood-corpuscles but in the proportion of 1 to $15\frac{7}{9}$ths. It is proper to observe that the animals which were the subjects of experiment at the two epochs, were not the same, the Bombinator igneus (*Rana bombina*, Lin.) having been examined in the autumn, and either the Rana temporaria or the Rana esculenta, in the early spring. R. W.]

[192] These corpuscles of the lymph, known to Leeuwenhoeck and especially to Hewson, were first more particularly described by Müller and called lymph-corpuscles; vide Burdach's *Physiologie*, iv. S. 108. Recent physiological writers generally agree with Müller in his views.

[193] Mandl, for instance, *Anat. Micros.* liv. i. p. 15, calls them "globules fibrineux," and Weber, Müller's *Archiv.* 1838, S. 450, follows him. See farther on under § 123.

brata[194]. We shall have occasion to revert to the probable significance of these corpuscles, and to speak of their relations to the proper blood-discs.

Besides the proper blood and lymph-corpuscles now mentioned, we constantly observe in whipt blood, scantily scattered here and there, a number of very minute molecules,—rounded globules, the 1000th of a line and less in diameter,[195] and also, but certainly very rarely, free fat-globules[196].

[194] I regard the corpuscles of the circulating fluid of all invertebrate animals as mere chyle-corpuscles; true blood-corpuscles do not seem to be formed in this division of the animal kingdom. I shall have more to say on this point by and by.

[195] These very minute globules are perhaps nucleoli of the lymph-corpuscles, around which other molecules may be deposited in layers; or perhaps they are the elements of disintegrated blood-corpuscles. They have been observed and described by Mandl, loc. cit. [In his very careful and long-continued studies of the fluid elements of animal bodies, Mr. Gulliver has discovered that the basis of the chyle is *a peculiar* molecular or granular mass, not to be confounded with the small spherules existing in various animal fluids, or with the few minute molecules of very different sizes, figured by Professor Wagner in the chyle; for the "molecular base," as described and depicted by Mr. Gulliver, is composed of particles very uniform in size, (fig. CXLIX.); it preponderates over the liquor chyli, constitutes the bulk of the chyle during digestion, is therefore the cause of the characteristic colour and opacity of this fluid, and can scarcely be distinguished with a magnifying power of less than 600 or 700 diameters. See Appendix to Gerber's *Anatomy*, p. 89. The molecular base of the chyle is very soluble in ether, whereas the minute spherules of the chyle, blood, and some other animal matters, are not affected by this reagent. Even the oil-like spherules of milk and of the supra-renal glands are not dissolved by ether. Microscopic observations on the minute particles of the chyle are not quite satisfactory without the aid of chemical tests. Mr. Gulliver has found the molecular base of the chyle in the venous and arterial blood both of young and adult animals. R. W.]

[196] Nasse occasionally but very rarely found oil globules in the fresh blood of

Fig. CXLIX.

Fig. CXLIX. Molecular base of the chyle on a micrometer scale of $\frac{1}{4000}$th of an E. inch. The four pale globules represented upon the ground are chyle-corpuscles. The average diameter of these is about $\frac{1}{4600}$th, and the molecules of the base are from six to eight times smaller, viz., from $\frac{1}{36000}$th to $\frac{1}{24000}$th of an E. inch.—*Gulliver*.

Formation of the Blood-Corpuscles.

§ 96. The blood-corpuscles are produced originally in the germinal membrane of the embryo; through the rest of life they are formed in the blood from the chyle. Like the phenomena of evolution generally, which can only be ascertained by extensive series of observations on parts in every stage of their progress towards completion, it is extremely difficult to seize the blood-corpuscles in their beginnings, and to follow them through their after-stages. If we examine the blood-corpuscles in half or in fully formed embryos, we perceive no difference between them and those of the grown animal of the same species. At the most, the only point of difference is some slight variety in respect of size. But if we select very young embryos as the subject of our studies—embryos of man, and the mammalia, of a few lines in length, or embryos of birds during the third day of incubation—we discover many blood-corpuscles in process of formation, [blood-corpuscles, at all events, very different from those of the maturer embryo and independently existing animal]. These blood-corpuscles are generally considerably larger, often twice larger than those of the fully-formed animal, and present themselves in the shape of soft, roundish, but often irregular bodies, of a pale red colour (fig. CL. *d*, and CLI. *b*), in which a distinct nucleus is very frequently visible without addition of any kind (fig. CL. *d*), or that can readily be brought into view by the use of reagents (fig. CLII). By the side

the dog. Vide his *Inquiries, physiological and pathological (Untersuchungen zur Physiologie und Pathologie*, Bd. ii. S. 187.) [Mr. Gulliver sometimes found oil-like particles in the blood of the feræ (Gerb. *Anat.* App. p. 23. R. W.]

Fig. CL.

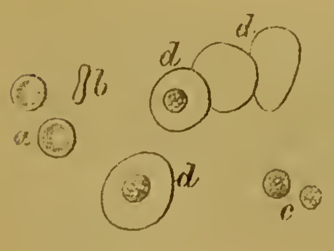


Fig. CL. Blood-globules of the embryo of vespertilio murinus; *a*, *b*, perfect globules; *c*, lymph-granules; *d*, *d*, blood-globules in progress of development from very young embryos; these are large elastic vesicles, many of which include a distinct nucleus. [See the parallel observations of Mr. Gulliver, at p. 240, fig. CXLVIII. B and C. R. W.]

of these larger bodies, and fully-formed normal blood-corpuscles, are perceived (fig. CLI. *a*), and farther, smaller, round, and frequently granular globules (fig. CL. and CLI. *c*). These last globules or granules appear to be nuclei of blood-corpuscles, which by attracting and aggregating vitellary elements, gradually surround themselves with a capsule—the future capsule or investment of the perfect blood-globule. Direct observations give us assurance of this. According to other observers, the vitellary globules or cells

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Fig. CLI.

Fig. CLI. Blood-globules perfect and in progress of development from the chick of the fourth day; *a*, *a*, fully formed globules, *b*, *b*, *b*, *b*, globules in process of formation; *c*, smaller, rounded granules, analogues of lymph-granules.

Fig. CLII.

Fig. CLII. Blood-globules of the chick that have been treated with water mixed with a little acetic acid; nuclei are conspicuous.

Fig. CLIII.

Fig. CLIII. Globules of the chyle, from the lacteals and mesenteric glands of a young woman, eighteen years of age, who had committed suicide by drowning. The body was inspected eight hours after death. A, Perfect chyle-globules. B, Smaller molecules, which are found swimming in the chyle, undoubtedly rudimentary chyle-globules. C, A chyle-globule surrounded with a very delicate envelope; in all likelihood in process of change into a blood-globule.

are themselves transformed into blood-corpuscles [197]; which of these views is the correct one has not yet been satisfactorily demonstrated.

Microscopic Analysis of Chyle and of Lymph[198].

§ 97. Chyle and Lymph consist like the blood of a homogeneous fluid, and certain peculiar corpuscles mixed with it. These cor-

[197] I have myself instituted researches on the early embryos of mammals, birds, and amphibia. According to Baumgärtner, *On the Nerves and the Blood, (Ueber Nerven und Blut,)* pp. 40, 80, 88, the blood-corpuscles in the embryos of amphibia and fishes are at first globular, and inclose other smaller globules within them; the blood-corpuscles themselves arise from the globules of the yolk; they gradually acquire a red colour, which is first observable when they have become elliptical; the earliest formed blood-globules, according to Baumgärtner, are compounded of many small vitellary globules, loc. cit. and Table viii. fig. 10—14. According to Schultz's account, which however is not very clear or comprehensible, clusters of vitellary granules become aggregated and included in a vesicle in the amphibia. In birds and fishes the formation of the blood-globules, he says, is different: here vesicles are formed around the individual vitellary globules. Schultz's *Syst. of Circulation*, p. 33. I see the figures in Schultz's second Table as very true to nature. Schwann regards the blood-corpuscles as cells, the nuclei of which are formed first, a capsule being then gradually formed around these,—the blood corpuscles are flattened cells, with nuclei attached at a point to the inner surface of the cell-membranes. *Mikroscop. Untersuch.* S. 76. Valentin is opposed to the idea of the transformation of the vitellary cells into blood-corpuscles. He views the blood-corpuscles not as cells, but as nuclei. The nuclei, in ordinary parlance, of the blood-corpuscles, he regards as nucleoli. Vide § 86, and Professor Valentin's *Observations*, at p. 214 et seq. [Vide also the addition to Annot. 184 and fig. CXLVIII. B. C].

[[198] To our countryman, Hewson, belongs the merit of having first ascertained from careful observations the nature of the lymph-globules, which he always called central particles (*Exp. Inq.* part 3, by Magnus Falconar, Lond. 1777). But Hewson's researches upon this subject were never properly appreciated; they attracted little or no attention, and were not once submitted to any examination fitted to ascertain their value. Yet the discoveries of Schwann, which involve the most important addition that animal physiology has lately received, fully confirm the accuracy of Hewson's views, and show that what he propounded in regard to the blood-corpuscles merely, is also applicable to the tissues, a fact which could scarcely have escaped observation, had the valuable inquiries of this ingenious man been continued with any zeal by his immediate successors. As far as the blood-corpuscle is concerned, the cytoblast or cell-germ of the German writers is but another term for the central particle of Hewson.

puscles of the lymph and chyle (fig. CLIII. A.) bear a strong resemblance to the second form of corpuscle met with in the blood (§ 95, *c* in figs). They appear to consist of an aggregation of molecules,

To the account given in the Appendix to Gerber's *Anatomy* (pp. 91 and 95—100) of the globules of the chyle, lymph, and thymous fluid, it may be added that the tissues during the early period of intra-uterine life are saturated with a juice scarcely distinguishable from that of the lymphatic glands of adults. The average-sized lymph-globules are indeed rather smaller and more regularly globular than those found in the embryonic tissues, but in the latter, the globules are already growing, while those of the lymph are only on their way to the blood just after their formation. In all other respects, these cell-germs of the fœtus are like those of lymph, and so numerous are they in some of the immature tissues as to render it probable that more globules are produced in certain organs than are necessary for their individual growth, as if they contributed to the formation of this embryo flesh and blood for the general increase of the body, until the special functions of such organs were called into action after birth. The fœtal lungs, for instance, are completely full of these cytoblasts or lymph-like globules, (fig. CLIV. B.) and so are the glands generally, and the spleen; and this latter viscus in the adult contains great numbers of similar particles.

As cell-nuclei may increase in size, it might be expected that the lymph-globules would become a little larger in the blood, and accordingly, as shown in fig. CLIV. C, the so-called lymph-globules of the blood are generally larger than those of the lymphatic juice, as I have observed in a great number of mammals and birds; and the pus-like globules found in the blood in many inflammatory diseases are still perceptibly larger than the ordinary pale globules of the blood. (See Gerber's *Anatomy*, fig. 269).

Hewson states that the particles of the fluid of the lymphatic glands of birds are oval, like the nuclei of the blood-corpuscles. But although the blood-corpuscles of the Napu Musk Deer and of the Camelidæ are quite peculiar both as to size and shape, I found that the globules in the juice of the lymphatic glands were similar to the globules of the like juice in animals with blood-discs of the ordinary size and figure; and more recent observations on the lymph of birds were to the same effect (fig. CLIV. A). It is remarkable, however, that the lymph-globules in many birds are smaller than the corresponding globules of mammals, while in the blood of the same birds, the so-called lymph-granules are quite as large as those of mammals. As to the opinion of M. Mandl that all the globules in question are nothing but particles of coagulated fibrine, it may be stated that as the fibrine is the plastic matter, it is difficult to suppose that cells or their nuclei are not derived immediately from it, since it has never been doubted that the mass of the coagulated lymph of inflamed parts is fibrine, and this coagulated lymph is now known to be chiefly made up of globules (see Gerber's *Anatomy*, fig. 243). In the following figures all the parts are represented as magnified 840 diameters, excepting only the pulmonary vesicles in B, which were drawn from a view with an object glass of one inch focal length

arranged about a central nucleolus which can readily be demonstrated by the action of acetic acid.

It is not rare to find indications of an envelope around these chyle-corpuscles (fig. CLIII. C), and every now and then, forms that appear very obviously to be transitions from the lymph into the

with the second eye-piece. The actual size of these vesicles was ascertained to be generally from $\frac{1}{200}$th to $\frac{1}{150}$th of an E. inch in diameter. G. G.]

Fig. CLIV.

A

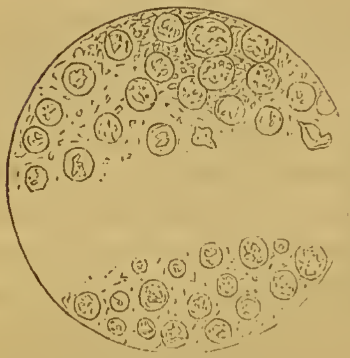
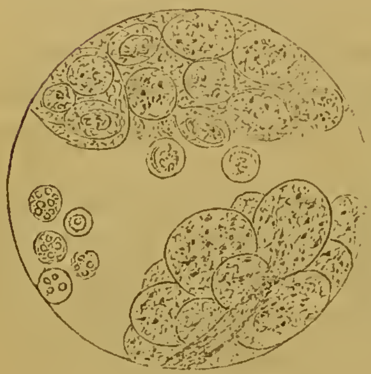


Fig. CLIV. A. Juice of the lymphatic glands of a common fowl. In the upper part of the figure the globules are floating in their own fluid, and in the lower part they are shown after being treated with acetic acid. Compare with the globules from the boy mentioned below, and with the lymph of the mammalia depicted in Gerber's *Anatomy*, figs. 279—287.

B



B In the lower part are seen, with a low magnifying power, pulmonary vesicles full of cell-germs like lymph-globules; in the upper part these globules are exhibited separately and highly magnified, as in the other figures. To the left are five of the cell-germs after they have been treated with acetic acid.

C

C In the upper part to the right are shown some lymph-globules from the juice of one of the cervical glands of a boy; to the left some pale white globules from the blood of a healthy man; in the lower half pus-like globules, some of which seem to include nuclei, from the blood of the right ventricle of a man twelve hours after death from erysipelas complicated with pleurisy. The relative size of the three varieties of globules is exhibited; their average diameters, in fractions of an E. inch, was observed to be as follows: viz., lymph-globules, $\frac{1}{4370}$th; the pale globules of the blood, $\frac{1}{3200}$th; and the pus-like globules $\frac{1}{2666}$th.

G. G.]

blood-corpuscle are encountered, the originally circular envelope (fig. CL. *d*), assuming an elongated oval shape (fig. CXLIV. *e*). The lymph-corpuscles may, therefore, with all propriety, be regarded as free nuclei of blood-corpuscles. [199]

Chyle and lymph are best and most readily procured in quantity for examination, by cutting through the turgid mesenteric glands of an animal just killed, and squeezing these over or against a plate of glass, when the fluids do not flow in drops of themselves. In this way, indeed, we have blood-corpuscles and the epithelial cells of the divided blood-vessels mingled with the proper corpuscles of the chyle, but these with a little practice are all readily distinguished from one another [200].

199 Many observers are in favour of this transition of the lymph or chyle-corpuscle into the blood-corpuscle. Nasse, among others, has treated of the matter fully. He says: "The different stages in the development of the blood-corpuscles, and the intermediate forms between the lymph-globules and these, are readily recognized in the elliptical blood-corpuscles, and cannot well be confounded with those forms of the blood-corpuscles that indicate degeneration. On the lymph-globule, to wit, a flattened rounded offset begins to grow from opposite sides, and increases gradually till it invests the entire globule. The larger, broader, and thicker these offsets become, the smaller grows the nucleus, so that the matter which forms the capsule is obviously derived from it. The capsule is in the first instance rather circular and paler, it is only by degrees that it becomes elliptical and redder. The corpuscle, mean time, is proceeding to acquire its characteristic qualities,—its length, breadth, and thickness,—as we find these in the majority of the fully formed blood-discs. The complete development of the capsular substance appears to commence and to proceed entirely within the blood-vessels in the animals mentioned [the frog, the newt ?] and to be accomplished very slowly." *Unters. zur Physiol.* ii. S. 183. These observations of Nasse accord entirely with my own, unless it be as regards the mode of evolution of the capsule, which he describes as *wing-like*, but which I have always seen to take place evenly around the lymph-globule as its nucleus. Valentin also considers the lymph-granules in the blood as nucleoli.

[These views are greatly strengthened by the fact already quoted, that the lymph-granules of the blood are very abundant during summer, and very scanty during winter in animals that hybernate, that they are numerous in the blood of recently fed animals, and rare in that of creatures which have been kept long fasting, &c. In the evolution of the blood-discs from the pale globules, Mr. Gulliver observed the envelopes either forming evenly around the globule, or in two opposite directions, and occasionally in a crescentic manner from one part only of the circumference of the globule. See Gerber's *Anatomy*, fig. 294. R. W.]

200 If we would procure chyle and lymph quite pure, we must take the one from the thoracic duct, the other from lymphatic vessels. I have found dogs the best

The corpuscles of the lymph and chyle swim like the blood-discs in a fluid that is comparable to the plasma or liquor sanguinis, but which is no subject for farther microscopical inquiries. Under the microscope it presents itself very much as a drop of blood does, the contained fibrine and albumen of which have been coagulated by the addition of a little alcohol [201].

Physico-Chemical Analysis of the Blood.

(BY DR. JULIUS VOGEL.)

§ 98. The proximate principles into which the blood may be resolved by chemical analysis are very numerous. A large proportion of the matters which the various organs of the body form, or which are encountered in the different secretions and excretions, is also met with as elements of the blood. This fact had been long suspected, for the blood not only supplies the materials for the formation and nutrition of all the parts of the body, but all the different secretions take place from it and at its expense, as it were. It is only in recent times, however, and since the study of animal chemistry has made such strides in advance, that this suspicion has by the aid of numerous experiments been reduced to certainty.

§ 99. So long as it is contained in the vessels of the living animal body, the blood, as we have seen, consists of a fluid—the liquor sanguinis or plasma, and certain solid parts which are suspended in this fluid, the blood-corpuscles. We shall begin by considering the chemical composition of the blood-corpuscles. These, in all vertebrate animals, are the bearers of the colouring matter which gives to the blood its characteristic red colour, and which by modern chemists is designated *Hæmatin* (Berzelius), or *Hæmatosin* (Lecanu.)

The hæmatin is not mechanically deposited in or upon the blood-corpuscles; it is chemically united with them, and may be readily

subjects for such experiments; the great glandular mass of the mesentery—the pancreas Asellii—in these animals also affords an abundance of chyle; and on the surface of the liver and spleen we commonly see turgid lymphatic vessels, by puncturing which we readily obtain their contents unmixed.

[[201] The very latest researches, which are those of Mr. Gulliver, show that this statement must be modified. The base of the rich chyle during the height of digestion is a white molecular matter, almost or completely obscuring the liquor chyli; but in poorer chyle the molecules may be seen to swim in the transparent fluid. See Annot. p. 247. fig. CXLIX.; and Gerber's *Anatomy*, App. p. 89—91. figs. 274—278. R. W.]

separated or removed from them by a variety of fluids, by none more effectually than by simple water, without their being thereby injured. In a state of absolute purity we are as yet unacquainted with hæmatin and its properties; we know, however, that it contains a notable quantity of iron, which appears indeed to be essential to its constitution, for hæmatin, by whatever method prepared, has still been found united with iron. For a long time the red colour of the hæmatin was ascribed to this combined iron; but this is a mere assumption which has never yet been proven[202]. If a portion of whipt blood to which water has been added be examined under the microscope, the blood-corpuscles will at first sight be supposed to have entirely disappeared,—this at least is the case with regard to the human blood; but after a more careful inspection of the field of view, particularly with the use of a high power and moderate light, they will be discovered again; but they are now extremely pale and almost completely transparent, the water having, in fact, dissolved the colouring matter out of them. If, however, we add a little diluted tincture of iodine, or better still, a saturated solution of iodine in common brine, the blood-corpuscles immediately become much more distinct, the iodine giving them colour. It is then easy to obtain assurance that they are nearly of the same size as before the addition of the water, and that they are not particularly altered even in the element of form. They only look somewhat distended or tumid. Under the prolonged action of water, however,—an action of several hours, or several days—they are dissolved and disappear entirely[203].

[202] In spite of all that has been accomplished, much undoubtedly yet remains to be done before the chemistry of the blood is exhausted. The subject is rather fully discussed in the systematic works of Müller and Burdach. In the *Animal Chemistry (Thier-Chimie*, 3te Aufl.) of Berzelius, in the *Medical Chemistry (Medicinische Chimie*, Freib. 1836, 2 Bde) of Fromherz, and in the *Manual of practical Medical Chemistry (Handbuch der angewandten medicinischen Chimie*, 1ter Band, Berl. 1840) of Dr. F. Simon, the latest and best information extant is contained. We have, besides, the monographies of Lecanu, *(Etudes Chimiques sur le Sang Humain*, Paris, 1837,) and of Denis, *(Essai sur l'application de la Chimie à l'etude physiologique du Sang de l'Homme*, Paris, 1838,) which deserve especial mention.

[203] The colouring matter of the blood, as it was investigated even by such chemists as Berzelius, Engelhart, Vauquelin, and Sauson, was more or less contaminated with other principles of the fluid, particularly by globulin and albumen. Le-

The colourless substance that remains after the abstraction of the colouring matter, and that forms the capsule of the blood-corpuscle, is a peculiar chemically characterized matter, which Berzelius designates by the name of *globulin*. It belongs to the class of albuminous principles along with albumen and casein. Lecanu, indeed, describes it as albumen, and Simon as a modification of casein[204]. We shall continue to speak of it in this place under its old name of globulin. In the large blood-corpuscles of the amphibia, we distinguish a third substance which differs chemically from both hæmatin and globulin; this is the substance which forms the nuclei of the blood-corpuscles. It is completely insoluble in water, and bears the greatest resemblance to albumen and fibrine

canu appears to have succeeded in procuring the principle in great purity (op. cit. p. 28 et seq.); but that the hæmatosin of Lecanu is the unchanged colouring principle of the blood does not appear to me to be demonstrated. Berzelius, too, doubts that it is so. The unaltered colouring matter, for example, as it exists in the blood-corpuscles, does not dissolve in the alkaline serum, but with great readiness in pure water; Lecanu's hæmatosin, on the contrary, is insoluble in pure water, but is readily soluble in water made slightly alkaline by the addition of potash or soda. The quantity of iron contained in the blood is very remarkable; Lecanu's hæmatosin contains 7,1 per cent. of metallic iron; the absolute quantity of iron present in the whole circulating fluid, however, is very small; in an adult it may amount in all to about ten grains. The state of combination in which the iron exists in the colouring principle of the blood has not been ascertained; in all probability the metal is actually combined with the organic radical of the colouring matter, an arrangement many parallels to which have been presented by the later organic chemistry. The various hypotheses in regard to the cause of the colour of the blood which Fourcroy, Treviranus, Hermbstadt, and others imagined, may be passed by in silence, their untenableness having long since been admitted.

[204] According to Berzelius, globulin approaches very closely to albumen, and like this last is precipitated from its solution in water by heat; but the coagulum is different from that of common albumen; it does not form flocks or a connected mass like this last, but is loose and granular. Another difference is, that globulin is not, like coagulated albumen, soluble in saline solutions. Simon (op. cit. p. 81) assimilates globulin to casein, and styles it *blood-casein*. It resembles casein in being precipitated by acetic and lactic acid from its solutions, and in being redissolved in an excess of each of these reagents; during the evaporation of a solution of globulin, too, it becomes covered on the surface with an insoluble pellicle, in the same way as a solution of casein. The differences from casein which it shows in its other relations are accounted for by Simon from its combination with hæmatin, from which it is extremely difficult to free it completely.

in the coagulated state; but it is distinguished from both in being either entirely insoluble or very difficultly and sparingly soluble in acetic acid. This nuclear substance is readily procured by digesting whipt frog's blood for a length of time with water; it then remains with the form of the nuclei of the blood-discs. That the same substance occurs in the blood-corpuscles of man and the mammalia, we conclude on analogical grounds; but that the fact is so has not yet been demonstrated by any direct experiment[205]. The corpuscles contain, in addition, a phosphoric fat, of the same kind that is found in the brain and nerves[206], and, like every other part of the animal body, a large quantity of water[207].

[205] Müller, Krause, and others admit nuclei in the human blood-corpuscles as well as in those of so many of the lower animals; analogy would lead us to say that this was probably so, but numerous experiments conducted with every regard to accuracy have failed to satisfy me that it is so. Simon (loc. cit. p. 38) declares the nuclear substance of the blood-corpuscles to be fibrine: he found that the nuclei of the blood-corpuscles of the frog isolated and dried, swelled up and became transparent under the agency of acetic acid. On treating the recent blood-corpuscles of the frog with acetic acid, I found that the contours of the nuclei remained for a long while very sharply defined and unaltered, whilst coagulated fibrine, treated with the same acid, examined under the microscope, immediately became perfectly transparent, and in a little while escaped the eye entirely. In trying the nuclei of pus-corpuscles, which, according to Simon, comport themselves like the nuclei of the blood-corpuscles, with acetic acid, I found the difference from fibrine which I have just indicated still more strongly marked. I rather incline, therefore, to regard the nuclei of the blood-corpuscles as coagulated albumen, a substance which is much more slowly affected by acetic acid than coagulated fibrine, were such an insulated reaction sufficient to characterize any substance chemically. According to Berzelius's view (loc. cit. p. 86) they are no albuminous matter at all, inasmuch as they are so slightly affected by acetic acid.

[206] That this phosphoric or phosphoriferous fat, which is obtained by treating the mass of blood entire, belongs to the blood-corpuscles in particular, cannot indeed be proved directly, but is rendered very probable from the fact that it cannot be procured either from the serum or from the fibrine by themselves; it must, therefore, exist in union with the corpuscles (Berzelius loc. cit. p. 91).

[207] Great obscurity being frequently the result of a vague and variable terminology, it will probably be held a service if I state in this place that Lecanu's *Hæmatosin*, the purest colouring matter of the blood yet obtained, is to be taken as of like import with Berzelius's *Hæmatin*; Berzelius's *Globulin*, again, the substance which remains after the colouring matter has been removed from the capsules of the blood-corpuscles, is very different from Lecanu's *Globulin*, which is only an impure hæmatosin mingled with some albumen; Lecanu regards the

§ 100. The *liquor sanguinis* or *plasma* in which the blood-discs are suspended, displays a still greater degree of complexity in its chemical composition than these. Besides water, which constitutes about three fourths of its entire weight, its principal constituents are albumen and fibrine, each of them in the fluid uncoagulated state. The fibrine coagulates spontaneously almost as soon as the blood is removed from the vessels of the living body; the albumen is in such quantity that the serum in which it is dissolved sets into a solid mass under the influence of a certain temperature[208].

capsular substance or Berzelius's globulin as identical with albumen. Simon's *Blood-casein*, on the contrary, is identical with Berzelius's globulin, and must not be confounded with the casein which L. Gmelin detected in the blood (see the next paragraph). By the *Red matter of the blood* (Blut-roth), finally, Berzelius does not understand the pure colouring matter of the blood, but a mixture or combination of hæmatin and globulin; the whole of the constituents of the blood-corpuscles together, consequently, with the exception perhaps of the nuclei and the fatty matter.

[208] The fibrine and albumen are the two most important constituents of the liquor sanguinis; in the formation and nutrition of the body they both play a distinguished part, and are of the last importance in the physiology of the animal body. It will not, therefore, be amiss to consider each in itself, and both in their mutual relations, a little more closely. In their fluid and uncoagulated states albumen and fibrine are sufficiently characterized and readily to be distinguished from one another: fibrine coagulates spontaneously shortly after its escape from the vessels, within which it circulates dissolved in the blood; albumen, on the contrary, never coagulates spontaneously; but it sets on the application of heat, on the addition of the greater number of the mineral acids, of many metallic salts, of tannin, &c. with each of which it enters into combination. In the coagulated state, on the other hand, the two substances are either no longer to be distinguished, or scarcely to be distinguished from one another,—at all events, every means hitherto devised to discriminate between them, must be allowed to be incomplete; probability but not certainty may be had that a certain substance is albumen, not coagulated fibrine, or fibrine, not coagulated albumen. Once coagulated, they cannot again by any chemical means be brought back to their original uncoagulated state; they dissolve indeed in acetic acid partially, and in alkalis—potash particularly, completely; but the solutions so procured have lost the property of coagulation either spontaneously or by the application of heat. The chemical composition of both substances, as discovered by elementary analysis, is also very much the same: both contain carbon, hydrogen, azote, and oxygen, almost precisely in the same proportion. Both alike contain small but constant admixtures of phosphorus and sulphur. Mulder has, therefore, very lately viewed both substances as combinations of one and the same radical, which he denominates PROTEIN, with phosphorus and sulphur. Ac-

The liquor sanguinis farther contains some casein, animal extractive—osmazom and salivary matter or ptyalin—a name under which are comprehended hitherto undecompounded mixtures of various substances not yet sufficiently known; a yellow colouring matter; urea in very small quantity (indeed whether this substance exists at all in perfectly normal blood is questionable); various kinds of fat, viz. cholesterin and serolin, free oleic and margaric acid, [209]

cording to him, albumen is a compound of ten atoms of protein with two atoms of sulphur and one atom of phosphorus; fibrine, again, of 10 atoms protein with 1 atom sulphur and 1 atom phosphorus. They only differ, consequently, in the one containing 1 atom sulphur more than the other. My own experiments have led me to results somewhat different from those of Mulder. I always found that the fibrine of the ox's blood contained rather more azote than the albumen of the hen's egg (*Annalen der Pharmacie*, 1839, April. S. 36.) [A very important quality of the plasma of the blood is the *viscidity* which it possesses in passing from the liquid to the solid form, as was long since particularly observed by Dr Davy (see *Researches*, *Phys. and Anat.* vol. ii, p. 239). So remarkable is this quality, that many forms of elongated morbid adhesions may easily be imitated by smearing the fingers with liquid coagulable lymph, and separating them as the substance becomes viscid, and before it finally clots. G. G.]

[209] Leopold Gmelin detected casein in small quantity in the liquor sanguinis. This casein, as already stated, is not to be confounded with the blood-casein, of which according to Simon the capsules of the blood-corpuscles consist. Casein is intimately associated with the albumen and fibrine in the blood, and according to Mulder is another of the protein compounds. This chemist, for example, regards the casein of cow's milk as a combination of 10 atoms protein with 1 atom sulphur; it only differs from fibrine consequently in the absence of phosphorus.

The substance spoken of as *animal extractive*, is a mixture of a number of animal matters soluble in alcohol and water; among the number, ptyalin or salivary matter, which is soluble in water only, has been indicated by Gmelin as existing in the liquor sanguinis. The other matters of the same class which are soluble in both water and alcohol, compose the osmazom of writers, itself a mixture of several not yet adequately characterized substances. Urea has been found by Prevost and Dumas, and by Tiedemann and Gmelin, in the blood of animals from which they had extirpated the kidneys; but neither these chemists nor Lecanu could detect any urea in the blood of healthy animals or man. Marchand, however, has either positively discovered urea in the healthy blood, or has rendered its presence there extremely probable (*Journ. f. Prakt. Chemie v. Erdmann*, Bd. xi. S. 449, und Bd. xiv. S. 490). This point demands renewed inquiry. [In the blood of persons labouring under disease of the kidney, urea has been frequently detected in large quantity (Bostock, in Bright's *Reports of Cases*, &c. 4to. Lond, 1827, Christison in *Edinb. Med. and Surg. Jour.* vol. xxxvii.

various salts,—sebacic acid salts, lactate of soda, hydrochlorate of potash, soda, and ammonia, sulphate of potash, carbonate of soda, of lime and of magnesia, and phosphate of soda, of lime and of magnesia; lastly, carbonic acid, oxygen and nitrogen, each in the gaseous state[210]. All these substances are dissolved in the liquor sanguinis, so long as the blood continues to circulate in the living body.

Besides the substances now mentioned, and those indicated in the preceding paragraph, different chemists have described other compounds still, as constituents of the blood; but these have either not been specified with such accuracy as to be again recognizable, or they appertained to diseased and altered blood[211].

1829, Willis, in *Lond. and Edinb. Month. Journ. of Med. Science*, vol. i. p. 697, 1841.) R. W.] The different kinds of fat of the blood have been indicated by Chevreul, Berzelius, Boudet, and Lecanu. Cholesterin is the highly crystalline fat which is found so abundantly in bile. Serolin appears to be peculiar to the blood; it is a fatty substance little soluble in alcohol, but readily soluble in ether, and which melts at a lower temperature than cholesterin. Oleic and margaric acid exist free in the blood, as was shown by Lecanu; as neither of these acids will decompose the carbonates, their presence is not incompatible with the simultaneous existence of these salts.

210 Of the salts, the compounds of chlorine, particularly common salt and sal-ammoniac, and the lactates, are encountered in almost all the animal fluids; but the alkaline carbonates to which the blood owes its alkaline reaction upon vegetable pigments, are peculiar to it. When with the commencement of putrefaction free ammonia is developed in the body, this unites with the phosphate of magnesia of the blood, and then we have microscopic crystals of the triple phosphate of ammonia and magnesia deposited in all the tissues. The subject of the presence of free gases in the blood will be discussed when we come to speak of the respiration.

211 The number of substances, in addition to those indicated above, which are said to have been found in the blood, is very considerable. It will not be superfluous briefly to run over the more important of them in this place, they being still constantly referred to in many chemical and medical works as constituents of the blood. The *subrubrine* of O'Shaughnessy (*Lancet*, Feb. 7, 1835) requires to be farther examined before it can be admitted as an immediate constituent of the blood. The chlorohæmatin and xanthohæmatin of Brett and Bird (*Lond. Med. Gaz.* vol. xvi. 1835) are obviously products of the decomposition of the coagulum by nitric acid, and therefore no immediate constituents of the blood. Fourcroy, Vauquelin, and others, assign gelatin as a constituent of the blood; but in recent times almost all inquirers seem to have agreed in declaring that this is not the case (Lecanu, loc. cit. p. 14). Sarzeau believed that he had found copper, and Wurzer that he had discovered manganese, in the blood; but if we

§ 101. The relative quantities of the different constituents of the blood will be best observed by turning to the following estimate of Lecanu. It is a table of the mean results of numerous analyses of blood obtained from men by venesection in the arm; from this it will be obvious that the numbers are approximative not real:

1000 parts of blood contain[212]—

1. Blood-corpuscles:		
Hæmatosin or colouring matter .	2,270	
Globulin or substance of the capsules	125,627	
		127,897
2. Liquor sanguinis:		
Water - - - - -	790,371	
Fibrine - - - - -	2,948	
Albumen - - - - -	67,804	
Free gases, oxygen, azote and carbonic acid; extractive matter, phosphoriferous fat, cholesterin, serolin, oleic and margaric acids, salts, yellow colouring matter, urea - - - -	10,980	
		872,103
		1,000,000

even allow the analyses of these chemists to have been correct, the quantity of these metals detected is so small and so little essential, that they can hardly be viewed as constituents of normal blood. Rees also thought that he had discovered titanic acid in the blood; but Valentin and Brunner, as might have been anticipated, could find no trace of this substance in their researches. [The blood ought to contain a great number of occasional and accidental ingredients at different times. Whatever can make its way into the body, in fact, and that is eliminated by any of the excreting organs, ought upon occasion to be found in the blood—neutral salts of various kinds, alkaline and metallic, either as they were taken by the mouth or in new shapes, the active principles or the saline combinations of these, met with in the vegetable matters which we use as food, physic, &c. All the accidental impregnations of the urine, of the halitus from the lungs, &c., must have been in the blood before they showed themselves in the secretion of the kidney, in that of the lung, &c. R. W.]

[212] The original statement of Lecanu has been slightly altered here, in order to meet the present state of knowledge in regard to the constitution of the blood. This chemist, for example, reckons the fibrine along with the blood-corpuscles; and until very recently, the same error runs through the analyses of French chemists generally; when they say "blood corpuscles," (globules,) therefore, the

This relation of the several constituents, however, is not always the same, it varies with the individuals, with the age, sex, and temperament of him from whom the blood which is investigated was drawn. Lecanu, for instance, found that in general the blood of adults of the male sex in the vigour of life, of persons well fed and of sanguine temperament, contained a larger proportion of blood-globules and of fibrine and a smaller quantity of water than are indicated by the above mean estimate. The blood of the female sex, on the contrary, of children and aged men, of subjects indifferently fed and in reduced circumstances, and of persons of a lymphatic constitution, was found poorer in blood-corpuscles and richer in water. The albumen and saline ingredients of the blood, again, were found under all circumstances pretty much the same[213]. The blood of the fœtus

fibrine is to be understood as included with the hæmatin. The work of Denis already referred to contains a great number of quantitative analyses of the blood in healthy and diseased states; but Denis assumes that the hæmatin combined with oxyde of iron composes the capsules of the blood-discs, and that the globulin, which he declares to be albumen, constitutes the nuclei of these bodies. According to him, the capsular substance amounts but to about the 100th part of the weight of the entire blood-globule, an estimate that is certainly and evidently erroneous; he maintains, moreover, that the colouring matter is a mere modification of albumen, and consequently reckons it in his analyses along with the albumen. It is conceivable how necessary it must be to have regard to these particulars, and how constantly the views of this chemist must be kept in view if we would compare the numerical results of his analyses with those of others or those we may institute ourselves. Another consideration is this: the generality of French analyses, the above mean estimate of Lecanu inclusive, place the whole of the water of the blood under the rubric, liquor sanguinis; but a certain proportion of it belongs obviously to the blood-corpuscles.

213 The very interesting numerical results of Lecanu's experiments upon the different quantities of water contained in the blood of the male and female sex, of persons of opposite temperaments, &c. are the following. The watery constituent of the blood of males in 1000 parts was in the maximum 805,263, in the minimum 778,625,—mean 791,944. The amount of blood-corpuscles and fibrine in the same quantity of the same blood was in the maximum 148,450, in the minimum 115,850,—mean 132,150. In females: water, maximum 853,135, minimum 790,394,—mean 821,764; blood-corpuscles and fibrine: maximum 129,999, minimum 68,349,—mean 99,169. In females of sanguine temperament, water (mean of four analyses) 793,007; blood-corpuscles and fibrine, 126,174, In females of lymphatic temperament, water (mean of five analyses) 803,710; blood-corpuscles and fibrine 117,300. The results in this direction in regard to the male sex are precisely similar: Males of sanguine temperament, mean of watery constituent 786,584; of blood-corpuscles and fibrine 136,497. Males of

and placenta fœtalis in a given weight was found to contain a larger proportion of blood-globules and less water than that of the mother[214].

§ 102. The blood shows important differences in the quantitative relations of its constituent parts in the course of different diseases. In plethoric states and in inflammatory affections it contains a larger quantity of fibrine and of blood-corpuscles and less water than in health. In chlorosis, in icterus, and in the course of diseases of the heart, it has a larger relative proportion of water and a smaller one of corpuscles. In jaundice it farther contains the colouring matter of the bile, a substance which is also almost always present in healthy blood in very small quantity; [In anuria, in certain diseases of the kidney, and in many cases of the dropsy that follows scarlet fever, the blood contains urea often in very considerable quantity; in diabetes mellitus it contains sugar;] drained of its water, in cholera, it contains a much smaller proportion of this fluid and a much larger one of albumen, fibrine, and corpuscles, than in health[215].

§ 103. The blood only continues fluid so long as it circulates in the vessels of the living body; removed from these it speedily passes from a fluid into a solid—it coagulates. This coagulation is effected by the fibrine, which is dissolved in and forms an element of the liquor sanguinis, passing from the fluid into the solid state,

lymphatic temperament,—watery constituent 800,566; of blood-corpuscles and fibrine 116,667. Farther details will be found in Lecanu's work, and in the interesting essay of Denis. The latter divides normal blood according to individual varieties, which depend principally on the amount of watery contents and the specific gravity, into four classes.

[214] Denis states this as the result of many analyses (op. cit. p. 238). The weight of the blood-corpuscles in fœtal blood exceeds the mean weight of the same element of female blood by at least one half, in some cases it was even as much as twice the weight of that of the mother.

[215] This subject plainly belongs to pathology rather than to physiology, so that it were improper to pursue it further here. The works of Lecanu and Denis, &c. may be referred to for more ample details. I have often satisfied myself that the colouring matter of the bile frequently exists in the blood of persons unaffected with jaundice. The serum of such blood has generally a yellowish-green colour; if a little nitric acid be added to it, the precipitated albumen as well as the supernatant serum assumes a grass-green hue, which with a farther addition of nitric acid passes into a blue, and by and by into a red, precisely as happens when diluted bile is treated in the same way.

and in doing so including in the first instance not only the whole of the suspended solid particles, the corpuscles, but the serum also. The coagulation of the blood is a purely chemical phenomenon, and is connected with no kind of vital process; it occurs in the course of from three to seven minutes after the blood has been drawn from a vein[216]. In the first instance the entire mass of blood

[216] The circumstances attending the coagulation of the blood as now described, were first made clear in recent times by the admirable experiments of Müller. Formerly the universal opinion was that the fibrine was contained in the blood-corpuscles, and that the crassamentum was formed by these adhering together and so forming a compact mass. It is easy, however, to obtain assurance that this old notion is incorrect, and on the contrary that the liquor sanguinis holds the fibrine in a state of solution during life. If a little blood be allowed to flow into a pretty thick solution of sugar in water, by reason of the great division of the fibrine an extremely delicate arachnoidal coagulum will be formed; this brought under the microscope, exhibits the blood-corpuscles unchanged, included in a transparent colourless mass, which is the coagulated fibrine. Farther, if the blood of a frog or newt, of which the corpuscles are very large and do not pass through the pores of fine filtering paper, be diluted with thin syrup and thrown on a filter, the corpuscles are arrested; the liquor sanguinis diluted with the sugar alone flows through. This fluid is clear, colourless, and contains no blood-corpuscles; nevertheless a coagulum is formed within it before long, as Müller first showed; whilst the blood-corpuscles that remain on the filter, if they be duly freed from adhering fibrine by washing with solution of sugar, remain loose, and unconnected. Lastly, the coagulation of the blood is prevented by all those means or agents that have the faculty of dissolving fibrine, viz. by the addition of acetic acid and of a caustic alkali to fresh blood. These facts demonstrate satisfactorily that the coagulation of the blood depends on the setting of the dissolved fibrine, not on the mere agglutination of the blood-corpuscles. [Nothing can be clearer than the description given by Hewson of the coagulable lymph, red particles, and serum. He says, " The crassamentum consists of two parts, of which one gives it solidity, and is by some called the fibrous part of the blood, or the *gluten*, but by others with more propriety is termed the *coagulable lymph;* and of another which gives the red colour to the blood, and is called the *red globules.* * * * That it is the coagulable lymph, which, by becoming solid, gives firmness to the *crassamentum*, is proved by agitating fresh blood with a stick, so as to collect all this substance on the stick, in which case the rest of the blood remains fluid. * * * In these sheets, by the *lymph* is always meant that part of the blood which jellies, or becomes solid spontaneously, when received into a bason, which the coagulable matter that is dissolved in the serum does not," &c. *Exp. Inq.* pt. 1, p. 5—6. Third ed. Lond. 1780. An interesting historical notice respecting the coagulation of the blood has been given by Dr. Davy, in his *Physiological and Anatomical Researches*, vol. ii. p. 49 et seq. The question whether the coagulation of the blood is a vital or

presents itself as a solid clot, for the reason specified; but by and by, the coagulated mass begins to shrink, and squeezes out the serous fluid which had been entangled in its meshes. The originally homogeneous mass is consequently now separated into two distinct portions; the one solid, the CLOT, CRUOR, or CRASSAMENTUM; the other fluid, the SERUM. The former has various degrees of consistency, is of a red colour, and consists of the fibrine which has coagulated and the entangled blood-corpuscles. The latter is a pale greenish-yellow coloured fluid, generally pretty transparent, but sometimes turbid in different degrees, and even milky[217], of a saltish taste, having a specific gravity between 1027 and 1029[218], and show-

merely chemical phenomenon is not yet determined. The recent observations of Gulliver (App. to Gerber's *Anatomy*, p. 14 et seq. Figs. 245—251) show that clots of fibrine have a rudimentary appearance of organization. Even when coagulated out of the body, fibrine contains corpuscles which would appear to be organic germs. This fact is very interesting, not only as concerns the nature of the act of coagulation, but also in relation to some of the doctrines about inflammation. That this latter process is not necessary for the healing of wounds in the human body may be very readily believed, now it is ascertained that cell-germs, or at least analogous corpuscles, are formed in the blood by the simple act of coagulation. R. W.]

[217] This turbid and milky condition of the serum, which is occasionally observed in blood from individuals perfectly healthy, is generally connected with the presence of a large quantity of oil or fat suspended in the serum; it is particularly observed when the blood has been obtained at no long interval after a full meal of nutritious food. When the turbidity is great we can always, with the assistance of the microscope, detect a large number of oil-globules mixed with the serum, which otherwise appears as a clear and transparent fluid without any solid precipitate. [The milky matter found on the surface of the serum Mr. Gulliver ascertained to be identical with the molecular base of the chyle. (See p. 247, Fig. CXLIX.) He frequently observed this white chylous matter in the blood, both arterial and venous, of sucking and adult animals. The most extensive observations on the milk-like serum are those of Hewson, loc. cit. p. 141—155, who attributed the appearance to reabsorption of fat, and not to unassimilated chyle. His microscopical observations on the milk-like matter (p. 142) seem, however, to agree with those of Gulliver. The latter author mentions a semi-opaque whitish serum which he considers distinct from that mentioned above. R. W.]

[218] [This is probably stated too high. From Dr. Davy's observations on the blood of several mammalia, it results that arterial blood is of somewhat less specific gravity than venous, and arterial serum than venous serum. The specific gravity of arterial serum was from 1019 to 1030, the mean 1022; of venous serum the specific gravity was from 1023 to 1030, the mean 1026. The mean specific gravity of arterial blood was 1050, of venous blood 1053. R. W.]

ing alkaline reaction with vegetable blues. The serum contains all the constituents of the original liquor sanguinis, with the exception of the dissolved fibrine. If the blood-corpuscles begin to subside towards the bottom of the vessel in which the blood is contained before coagulation takes place, the upper stratum of the clot contains none of these particles, and is consequently of a white or pale yellow colour, and consists of pure fibrine ; this is the *buffy coat* of the blood, which is seen particularly in the blood of pregnant women, and of those who are labouring under acute inflammatory diseases[219]. In many diseases—in putrid fevers, &c. the blood which is let from a vein does not coagulate properly ; it either remains entirely fluid, or it sets partially or completely into a soft, tremulous jelly-like mass, instead of a proper clot, a phenomenon that must depend either on a deficiency of fibrine or on some chemical change having

[219] Mulder found the dried buffy coat to consist of fibrine with two and a half per cent. of fat. In the moist state, when it is still loaded with serum, it has been found to consist in 100 parts, of 3,02 fibrine ; 005 fat ; 8,78 fluid albumen ; and 88,15 water (Berzelius). The formation of the buffy coat may be explained in different ways—either the blood-corpuscles sink more rapidly than usual towards the bottom, or the blood coagulates more slowly than wont. In all probability the two circumstances co-operate in the generality of cases. [The most careful observations of recent date show a diminution in the specific gravity of the serum, or rather of the liquor sanguinis, as frequently connected with the occurrence of the buffy coat ; this lower specific gravity of course allows the blood-corpuscles to subside more readily than usual. Dr. Davy, however, believes, with Hewson, that the buffy coat is dependent on an increased fluidity or diminished viscidity of the coagulable lymph, as well as connected with its more tardy coagulation ; and that there is no necessary connection between the specific gravity of the blood and the presence or absence of the buffy coat. Thus in five instances in which the buffy coat was slight the specific gravities were 1047, 1051, 1055, and 1054 ; and in other five cases in which the buffy coat was moderately thick, the specific gravities were 1044, 1038, 1052, and 1056 ; and in an instance of thick buffy coat the specific gravity of the blood was 1057. It results from his observations generally, that the blood of persons labouring under acute diseases differs very little in specific gravity from healthy blood, and is of comparatively high specific gravity, or at least not below the mean, whether buffed or not. *Researches*, *Phys. and Anat.* vol. ii. p. 30—49. R. W.] The larger amount of fibrine which has been indicated in connexion with inflammatory diseases (Denis, l. c. p. 136) does not of itself explain the occurrence of the buffy coat ; it, however, explains one circumstance that is very commonly associated with this appearance, viz. that the crassamentum in such circumstances is generally firmer, denser, and more difficult to divide with a knife than usual.

occurred in its constitution, by which its coagulability has been lessened or destroyed. The blood does not coagulate out of the body only ; it also sets within the living frame when it is extravasated—in cases of effusion of blood into the bronchi, in apoplectic cysts, &c. we find the blood set into coagula similar to those that are produced without the body, though they may generally be somewhat softer perhaps than these last. Shortly after death the blood coagulates in the vessels, particularly the larger veins, and in the right cavities of the heart; in the capillary vessels, on the contrary, it remains fluid for several days after death, though it will coagulate speedily when removed from these. With incipient putrefaction the coagulating property of the blood is destroyed. It is not uncommon to find white or colourless coagula—coagula which contain no blood-corpuscles, in the heart; these are what are called false polypi. They are formed in all probability during the life of the individual; the absence of blood-corpuscles in their interior is readily to be explained, and is another evidence of their formation some time prior to death ; the columnæ carneæ, and chordæ tendineæ, aided by the motion of the heart, must act upon the blood precisely in the same manner as the switch with which freshly drawn blood is beaten when we would collect the fibrine from it.

Physico-chemical Analysis of the Lymph and Chyle.

§ 104. The chemical composition of the lymph is very similar to that of the blood ; as a general rule, however, it contains a larger proportion of water, and a smaller proportion of solid constituent parts than this fluid. Like the blood, the lymph consists of a fluid in which the solid elements, the *lymph-corpuscles,* are suspended. Accurate chemical researches into the nature of the lymph-corpuscles are still wanting ; in all probability they consist of a substance analagous to, perhaps identical with, the globulin of the blood-corpuscles [220] ; and the nuclei of the lymph-corpuscles may be found of

[220] [From Mr. Gulliver's observations it appears that saturated solutions of many earthy and alkaline salts after a while combine with and destroy the lymph globules, but, on the contrary, preserve entire the blood-corpuscles. The result of his inquiry is that the globules of the lymph, of the thymous fluid, and of the chyle have the same chemical characters (See Gerb. *Anat.* App. p. 79) ; but these globules differ in some respects from the nuclei of the blood-corpuscles R. W.]

the same essential chemical constitution as the nuclei of the blood-corpuscles when they occur. The hæmatin or red colouring matter of the blood is entirely absent in the true lymph-corpuscle [221].

The fluid of the lymph, besides water, contains fibrine and albumen as essential ingredients; also animal extractive (osmazome and ptyalin), fat and a variety of salts—carbonate, sulphate, and lactate of potash and soda, chloride of sodium, chloride of potassium, phosphate and sulphate of lime, and a trace of oxyde of iron. The quantitative relations of these various constituents in the human lymph according to Marchand and Colberg are the following:

Water	96,926
Fibrine	0,520
Albumen	0,434
Osmazom (and loss)	0,312
Oily fat, Crystalline fat	0,264
Chloride of sodium and of potassium, carbonate and lactate of potash, sulphate and phosphate of lime, and oxyde of iron	1,544
	100,000

The proportions of these constituents are not however always the same; experiments upon animals have shown that they differ, first, according to the organ from which the lymph is obtained; and

[221] In some earlier experiments I found that the envelopes of the lymph-corpuscles of the dog were dissolved in acetic acid, whilst the substance of the nucleus was not attacked by this reagent (vide Vogel, *Physiol. patholog. Unters. über Eiter*, *&c.* Erlang. 1838, S. 86). The lymph of several organs, particularly of the spleen, is commonly enough of a reddish tint, and according to Gmelin contains the true red-colouring matter of the blood. That this is in combination with the lymph-corpuscles does not appear to me probable; but whether the colour depends on admixed blood-corpuscles or upon a solution of their colouring matter in the liquor lymphæ, I cannot take upon me to say. [The spleen is in great part composed of pale corpuscles scarcely to be distinguished from those of the lymph. The chemical characters of the splenic and lymphatic globules are the same, and the only appreciable difference is that the globules of the spleen are a little more irregular in shape and size than those of the lymphatic glands. G. G.]

secondly, that they vary according to the quality and quantity of the food that is consumed [222].

The fibrine of the lymph coagulates, like that of the blood, when the fluid is removed from the containing vessels. The coagulum of the lymph, however, does not generally form a proper firm clot like that of the blood, but at the most an extremely delicate or arachnoidal mass in which the lymph-corpuscles are included. The serum of the lymph reacts, like that of the blood, pretty strongly in the manner of alkalis upon vegetable pigments, a property which depends on the alkaline carbonates it contains.

§ 105. The chemical composition of the chyle, despite the many researches we possess (by Tiedemann and Gmelin, Leuret and Lassaigne, Prout, Brande, Reuss and Emmert) is still all but entirely unknown. A connected satisfactory view of its composition is therefore impossible at the present moment; the statements of each and all of the experimenters mentioned are too defective, and mutually contradictory. What is actually known, however, is as follows:

The chyle of the lacteals at their origin, immediately after its absorption from the intestine, has not yet been chemically examined with due care. It has commonly a white colour and milky appearance, which, according to Tiedemann and Gmelin, depend on the presence of suspended oil-globules. It does not coagulate on exposure to the air when removed from the vessels, and therefore contains no fibrine. What chemical constituents it may contain has not yet been ascertained, to the best of my knowledge; even the corpuscle of the chyle has not yet been examined chemically [223]. The question

[222] The foregoing analysis of the human lymph by Marchand and Colberg, is the only one we possess. The lymph was obtained from a sore upon the dorsum of the foot which had obstinately resisted all the means used to heal it up (Müller's *Archiv*. 1838, S. 129). The quantity of fibrine is certainly too great. The entire coagulum, which undoubtedly contained lymph-corpuscles entangled with it, is set down as fibrine. [I should say that the analysis was rather that of an ichor or discharge from an open sore than of the lymph as we conceive it flowing in its appropriate canals. R. W.] In the lymph of the horse Lassaigne found:—Water, 92,500; fibrine, 0,330; albumen, 5,736; salts, 1,434. In the lymph of the frog Müller once found more than 1 per cent. of fibrine; the lymph of frogs that had been kept long fasting on the contrary contained no fibrine—it no longer coagulated. The statements in the text are to be taken as especially applicable to the lymph of the extremities and of the thoracic duct. The chyle of the intestinal canal is otherwise constituted; occasion to speak of this will be found when digestion is the subject of consideration.

[223] [Mr. Gulliver's observations on this subject are worthy of attention. As

—whether the food which has undergone solution and chemical change in the stomach is taken up by the beginnings of the lacteal vessels, as it is, or whether it suffers a farther change during the transference, cannot consequently be answered. There are but two experiments of Tiedemann and Gmelin that bear on the point. They found that the chyle of an animal which had been fed on butter was richer than usual in fat, and that the chyle of a dog which had been fed on starch, contained sugar.*

These statements are all obviously in favour of the absorption of the fluid parts of the chyme unaltered; but they will probably be held as very far from conclusive on the matter. They are the solitary observations we possess that the chyle varies with the qualities of the food; all other observations, those of Tiedemann and Gmelin inclusive, extend no farther than an indication of the different colour and general appearance of the chyle, from which no satisfactory inferences can be drawn with regard to chemical composition especially. The chyle is alkaline, whilst the chyme contains free acids; it is unknown how this difference of chemical constitution is brought about.

As the chyle advances along the lacteal vessels, as it passes through the mesenteric glands and finally reaches the thoracic duct, it undoubtedly undergoes chemical changes and becomes ever more and more like blood. It now coagulates spontaneously, and therefore contains fibrine; its serum also sets in a greater or less degree under the agency of heat, and consequently contains albumen. Upon this interesting topic there are unfortunately many gaps in the researches of Tiede-

already noticed, he could find no difference between the chemical characters of the globules of the chyle and lymph. He occasionally saw a delicate coagulum in chyle from the peripheral lacteals. See his *Observations on the Chyle*, &c. in the Appendix to Gerber's *Anatomy*. Lond. 1841. See also the able article, LYMPHATIC AND LACTEAL SYSTEM, by Mr. Lane, in the *Cyclopædia of Anat. and Physiol.* where there is an analysis of the chyle by Dr. G. O. Rees. R. W.]

* Brande also states that he had discovered sugar of milk in the chyle, Berzelius *Thierchemie*, alte Aufl. S. 273, [and Gerber (*General Anat.* p. 60) tells us that upon one occasion he discovered starch in the chyle of a horse by the ordinary iodine test. My friend Mr. Gulliver informs me, however, that he has searched for starch in the chyle of dogs fed upon amylaceous matters, but in vain. R. W.]

mann and Gmelin: several times they state that the serum of the chyle is completely or incompletely coagulated by heat; but in the majority of instances there is no mention made of the matter, so that we are in ignorance whether they failed to discover albumen, having sought for it, or whether they did not think of looking for it at all. The chyle in this part of its course is, farther, commonly enough of a reddish colour, and therefore contains the colouring matter of the blood. (Tiedemann and Gmelin's test for this substance, sulphuretted hydrogen, which turns hæmatin green, is not altogether to be depended on.) The quantities of these three substances contained in the chyle are so variable that it were useless to give the results of the various quantitative analyses that have been published. How or in what way is this chemical change effected in the chyle? This question has hitherto only been answered by hypothesis. The reply to it indeed presents a kind of two-fold difficulty, for we have not yet any precise information as to what this change consists in —comparative quantitative researches on the altered and unaltered chyle are still desiderata. 1. The change is effected by means of a biochemical action of the walls of the lacteal vessels, and particularly of the lymphatic glands, upon the chyle. It was supposed that the fibrinous contents of the chyle could be accounted for in this way, a portion of the albumen of the fluid being presumed to be gradually changed into fibrine. 2. The change is effected by the action of certain substances separated from the blood. 3. The contents of the chyle in regard to fibrine, albumen (?) and colouring matter, depend on admixed lymph. This last view is plainly untenable; for were it even allowed that some small portion of the whole amount of each of the three principles discovered in the chyle was derived from mingled lymph, the largest portion must still be held as derived from the aliment; what were the object of the chyle at all, did it contribute nothing towards the supply of the constituent elements of the blood? or shall we suppose that the assimilation is first accomplished in the blood itself, particularly in its passage through the lungs, as some writers have maintained? My own opinion is, that the matters consumed as food undergo no such great change as is commonly believed. The aliment of man and of the greater number of animals contains fibrine, albumen, fat, even the red colouring matter of the blood, in a word, the greater number of the constituents of the blood; these are dissolved in the stomach

without suffering particular change in their chemical composition. The assumption that albumen, for instance, should become changed into osmazome and ptyalin, is obviously a backward step in the knowledge we have of the processes of digestion and nutrition. But the alimentary matters dissolved in the stomach require to experience no very great amount of chemical change to pass into constituents of the blood; the greater number of the constituents of the food of man and animals belong to the family of protein-compounds, which have an uniform and precisely similar elementary composition. The vegetable albumen which is so main an ingredient in seeds of every description, and particularly in those of the cerealea, is referable to the class of protein-compounds, and according to Mulder, is almost identical with animal albumen. The formation of the chyle [and from this of the blood and the entire body] is, it must be allowed, much more difficult of explanation in the graminivorous animals, [and in those that live on the saccharine principle, of which there are whole tribes.] We shall probably only understand this difficult matter when we shall have fathomed the process by which vegetables form albumen from matters that contain no azote[224].

[224] [The very recent researches of Liebig and his school have thrown the greatest light upon almost every one of the topics hinted at in the preceding paragraph. Vegetables appear to be the creators or compounders, animals the destroyers or decompounders, in the organic realm of nature. Animals are in fine universally dependent on vegetables for every principle that enters into the constitution of their bodies, either deriving these principles from the vegetables on which they live immediatcly, or procuring them mediately through the body of another animal, having no power of forming anything, but merely of appropriating. Vegetables, again, under the influence of the sun's light, decompose the carbonic acid which is thrown off so abundantly by animals, and is a regular constituent of the atmosphere, fixing the carbon, that principal ingredient in their constitution, and setting free the oxygen. Vegetables, moreover, have the power of fixing azote either directly from the atmosphere, or more commonly by abstracting this element from nitrogenous compounds, especially the salts of ammonia, which are evolved so copiously by the decomposition of the effete matters and dead bodies of animals. Vegetables, in short, do not form their azotised principles, which are found to be much more constantly and copiously present in their composition than was once supposed, from matters that contain no azote ; they require supplies of aliment as much as animals. It is most interesting to know that the whole of those principles which are most universally used as food by animals—vegetable albumen, legumen or vegetable casein, and gluten or vegetable fibrine, have all precisely the same elemen-

CHAPTER II.

OF THE CIRCULATION OF THE BLOOD AND THE VASCULAR SYSTEM.

General Considerations.

§ 106. The juice or fluid which is separated from the food by the process of digestion,—the chyle, and the lymph and proper blood, are distributed to every part of the body through appropriate channels, and so brought into contact with all the organs and their elements. This distribution of the nutritive fluid is spoken of under the general title of *The Circulation of the Blood;* the organs and canals by means of which and through which it is accomplished constitute the *vascular system.* It is of peculiar importance to be familiar with the general morphology of the vascular system in the animal series ; it is by a study of this kind that we become acquainted with the individual elements from which the vascular system of man and the higher vertebrata is compounded[225].

tary composition as the corresponding animal principles, or as dry muscular flesh or blood; they consist severally of about 54 carbon, 15 azote, from 6 to 7 hydrogen, and from 21 to 23 oxygen, phosphorus and sulphur in 100 parts. Animals, consequently, even when herbivorous, receive the constituents of their bodies ready prepared for them; they but appropriate, they compose nothing. The carbon which is so essential an article of aliment, and of which the grand representatives in the food of man and animals, are starch, sugar, and oil or fat, is principally used up in respiration; it is literally burned in the animal body as coal or coke is in a furnace, and with the same effect, the evolution of heat, whilst it is converted into carbonic acid. The azotised elements of food again go to the constitution of flesh, membranes, ligaments, &c., and as *change* is the condition connected with the manifestations of life, seem to be principally eliminated in the shape of urea by the kidney. R. W.]

225 The discovery of the circulation of the blood is the line of demarcation between the old and the new physiology. William Harvey is universally acknowledged to have been the discoverer of the circulation. After testing his discovery in many ways for a number of years, he announced it publicly in his lectures delivered in London in 1619, and in 1628 it was made known to the world at large by the medium of the press, he having published his work entitled *Exercitatio Anatomica de motu Cordis et Sanguinis in Animalibus*, at Frankfort in the course of that year. Malpighi was the first who actually *saw* the circulation of the blood in the lung of the frog placed under the microscope,—*De Pulmonibus*, *Epistolæ duæ*, *ad Borellium*, Bonon. 1661. Among the more recent works which treat especially or exclusively of the circulation, the following deserve particular mention: Döllinger,

Vascular System of Vegetables.

§ 107. All the nutritive matter which vegetables assume is dissolved in water, is absorbed by the root, and rises from cell to cell to every part of the plant. The dissolved substances remain in the body of the plant, whilst the menstruum in which they are dissolved, the water, is in great part thrown off or dissipated by exhalation. The juice that circulates in this way is spoken of as the *crude sap,* and in the most perfect plants, or those in which the bark and woody body are separate and distinct, it ascends from the roots to the extreme parts through the latter. According to older but now disputed views, the sap, after having reached the extreme parts of the plant, proceeded in a retrograde course through the bark. The ascent of the sap takes place most vigorously in the early spring, and in no vegetables more strikingly than in the birch and vine, in either of which a wound or a branch cut across pours out a profusion of the nutrient fluid, the stream flowing from the divided cells, but still more from the spiral vessels. At a later period, when the leaves are fully expanded, the spiral vessels are found empty or containing but very little sap. In those vegetables that have no absorbing roots, such as lichens, algæ &c., the sap is taken in from the surrounding medium by the entire surface, and is then conducted away from cell to cell.

Besides this general permeation of the whole elementary structures of vegetables by the crude sap, there are other especial circu-

On the Circulation of the blood (Ueber den Kreislauf des Blutes; in Denkschr. der Münchner Akademie, Bd. viii., 1820); Oesterreicher, *An Essay towards an Exposition of the Doctrine of the Circulation (Versuch einer Darstellung der Lehre vom Kreislaufe des Blutes;* Nürnberg, 1826); Wedemeyer, *Researches on the Circulation of the Blood (Untersuchungen über den Kreislauf des Bluts*, Hannov. 1828). The two most important works of the day, both of which contain excellent plates, are Dr. M. Hall's *Critical and Experimental Essay on the Circulation of the Blood*, Lond. 1831, and Schultz's *System of the Circulation (System der Circulation*, Stuttg. 1836). In the following exposition I make abstraction in as great a degree as possible of all inquiries into the causes and means by which the circulation of the blood is effected, and the phenomena immediately connected with these, such as the motions of the heart, the pulse, &c., &c., conceiving that this portion of the subject will be more naturally treated of in connection with the organs of motion, and as it is obviously without peculiar interest in the consideration of the processes of nutrition.

latory or rotatory phenomena going on in the interior of the particular cells, which appear to stand in the most immediate relationship with the assimilatory processes of vegetables. This rotation of the sap is particularly distinct and remarkable in the different species of Chara, which are composed of a series of simple superimposed cells. Here the numerous larger and smaller globules which are contained in the sap are seen to rise along one side of a cell, to turn round at the roof, to descend along the opposite side, to proceed along the floor and again to join the ascending stream. All the while neither contraction of the parietes of the cell, nor ciliary movement of any kind, can be detected as the efficient cause of the current. Similar phenomena have lately been observed in many other vegetables, the motions extending even into the finest articulated hairs, so that the majority of plants appear to have a circulation of the sap appropriate to each particular cell.

The third kind of motion of the sap is that which is entitled *Cyclosis*, and bears reference to the motion of the *cambium*, or milky juice, a vital fluid analogous to the blood of animals, and prepared in all probability from the crude sap. This circulation is to be observed most readily and distinctly in plants that have opaque milky juices, such as the greater celandine, (Chelidonium majus), the fig, &c. The cambium moves in peculiar vessels, formed of extremely delicate and transparent membranes, which branch off or ramify like the blood-vessels of animals, and anastomose freely with one another. The distribution of these vessels is particularly obvious in the leaves. The continuity of the vessels that circulate the cambium through the entire vegetable has not yet been satisfactorily demonstrated; but it has very recently been maintained that the cambium ascends in a few principal trunks, which run parallel to one another in the circumference of the stem, from the roots to the leaves, that it courses through the innumerable ramifications in these, and returns through their finest subdivisions to make its way into larger vascular trunks, which run down the stem, and from this lead back to the roots, all the divisions of which they follow; here the cambium receives an accession of crude sap, and then the circulation begins anew.

§ 108. It would appear, then, according to the views now entertained by phytologists, that there are three motions of the sap in vegetables: 1st, *A motion of the crude sap*, which consists principally

of water, loaded with the soluble matters that are contained in the humus, which is taken up by the root or the surface generally, which spreads through the entire parenchyma, ascending and then evaporating in very great measure in the leaves, and also again descending in part within the cells of the alburnum. 2nd, *A motion of a sap proper to the cells,* a circulation restricted to each individual cell, of the description already indicated. 3rd, *A circulation of the cambium,* which goes on in a special system of vessels, analogous to those of animals, and distributed through the entire plant. In what relationship these three apparently principal motions of the sap stand to one another, and what their import may be with reference to the assimilatory process in vegetables, are points that have not at the present hour been explained. It is, however, of particular interest as regards animal physiology, that in vegetables there is, 1st, A regular motion of fluids independently of the agency of any special motory organ, such as heart, cilia, &c.; and 2nd, That the composition and distribution of the juices bear very decided analogies to those of the chyle and the blood[226].

[226] The accounts we find in the writings of phyto-physiologists of the motions of the sap are highly contradictory and puzzling. The best general views we possess are probably those given by Bischoff in his *Elements of Botany (Lehrbuch der Botanik*, B. 2. S. 260), where the known and approved observations are exposed with much brevity; and by Meyen in his *New System of Vegetable Physiology (Neues System der Pflanzenphysiologie)*, where numerous original observations are contrasted with various others of older date. The *crude* sap and its ascent were well known to the old enquirers; the saccharine juice of the birch and maple, which may be collected in large quantity in the spring season before the unfolding of the leaves, by perforating the trunk of the tree, is regarded as a crude juice, which has, however, already undergone some change in the course of its ascent. The sap of the vine is perfectly limpid, almost tasteless, very watery, and flows in the spring before the leaves have burst, from every wounded part of the plant in great abundance. The superfluous water evaporates in the leaves; the nutritive matter, extract of humus, which consists in great part of carbonic acid, remains behind. Under an elevated temperature and sunshine the ascent of the sap goes on more rapidly than in cool and cloudy weather. In the cellular plants—mosses, lichens, &c.—an ascent and retrograde motion of the sap has not been observed with certainty; neither has anything of the kind been seen in cryptogamic vascular plants, the monocotyledones and herbaceous dicotyledones. On the other hand, it used to be universally admitted that in the dicotyledonous trees and shrubs, in which wood, alburnum, and bark are always distinctly separate, the ascent of the sap took place principally in the wood, the descent in the cortical parts—the alburnum and proper bark. But Meyen will

Morphology of the Vascular System in the Animal Kingdom.

§ 109. The general morphology of the vascular system of animals supplies us with many interesting subjects of contemplation. It

not allow that this descent or reflux of the sap is in any way proven; on the contrary, he maintains it to be very improbable. It would nevertheless appear that the elongated sap cells of the alburnum contain a more highly organized nutritive sap (cambium). It is extremely interesting to watch the motion of the sap in the elongated and somewhat spirally twisted canals of the cells of the chara flexilis and chara vulgaris. Corti discovered this phenomenon in 1772. *Osserv. micros. sulla Tremella e sulla circolazione del fluido in una pianta acquajuola*, Lucca, 1774. It has been frequently described since; particularly by Amici, in his *Obs. micros. sur diverses espèces de plantes*, *in the Ann. des Sciences nat.* ii. p. 41 (1824) from the *Atti della Societa Italiana*, T. xix.; by Agardh in his paper on the Anatomy and the circulation of the Chara in *Nov. Act. Acad. Leopold. Nat. curios.* vol. xiii. P. I. p. 115.; and by Bischoff in the first number of his work on the Cryptogamia *(Kryptogamische Gewächse)*. This peculiar circulation is visible in almost every part of the chara, particularly when the temperature is genial, but the rotation of the sap within the cells is most beautifully displayed in the very delicate hairs of the roots. Meyen (loc. cit. ii. 207) has given a good account of the different phases and conditions of the phenomenon, and also of the numerous researches of different observers. Motions similar to those of the Chara have been recently discovered in the Vallisneria, Najas, and particularly in the hairs at the bases of the anthers of the Tradescantia Virginiana. Here there is not merely a simple stream in each cell perceived; the stream divides into many small branches, which again unite with the principal stream. Schleiden (Linnæa, 1837, S. 527) discovered in the cells of the endospermium of the Ceratophylli a peculiar cellular circulation not of the usual general parietal kind; the stream rose from the bottom of the cell like a *jet d'eau*, and divided on the roof into innumerable fine and scarcely visible branches, which fell down again upon the wall, to unite once more below with the principal ascending current. Meyen maintains that rotations of the cellular sap of vegetables are by no means restricted to those that have been particularly indicated as exhibiting them, but may be seen in the delicate and transparent parts—the hairs of the radicles, for example, of all the higher and even of many of the lower vegetables. The milky juice (cambium) appears to be prepared in the leaves from the crude sap, and from them to be transmitted to the wider canals, entitled sap ducts, which course between the cells, not only of the bark and alburnum, but of the interior of the stem, also in the leaf stalks and ribs, and frequently communicate by means of transverse canals. The cambium contains globules, and is an emulsion in water of finely divided resinous and oily substances, the vehicle at the same time holding various salts in solution. It is sometimes deeply coloured, of a deep yellow, for example in the celandine, reddish in the sanguinaria, brownish-green in hortulaca oleracea, more or less white and opaque in a great number of plants, as in the figs, eu-

may be said that two principal forms of the vascular system are encountered in the animal series, each of which resolves itself into several sub-divisions.

I. *Mere Chyle*, not proper blood, circulates in a vascular system of very various structure. This is the circulation that obtains in the invertebrate series of animals.

II. *Proper Blood*, a red coloured fluid containing characteristic corpuscles, circulates through a vascular system consisting of a heart, arteries, veins, lacteals and lymphatics. This is the circulation that obtains universally in the vertebrate series. The invertebrata, again, fall into three groups, in conformity with their physiological relations to the circulating system. 1. Animals having simple chyliferous vessels, taking their rise from the stomach and being distributed to the substance of the body without any trace of a heart, the nutritive fluid here consisting of a lymph having irregular granules mingled with it, and being carried along by ciliary motions,—by the action of cilia attached to the parietes of the vessels. To this first group belong, according to present observation, polypi, medusæ, and many worms, particularly the Entozoa. 2. Animals in which the chyle, transuding the intestine, bathes all the viscera of the body, and is then collected into a dorsal vessel (a heart) furnished with lateral clefts for its reception, from which it is again shed into the various cavities of the body through a simple or ramified principal trunk. To this subdivision appertain insects of every kind, and a portion of the myriapods and crustaceans. 3. Animals with closed anastomosing vessels, analogous to arteries and veins, with superadded pulsatory muscular sacs or pouches (hearts), which, however, circulate chyle, not true blood. In this

phorbias, poppies, &c. Dr. E. H. Schulz was the discoverer of the circulation of the cambium, which he described at a later period under the title of Cyclosis. (Schulz *Ueber den Kreislauf des Safts im Schollkraut*, Berl. 1822. *Ueber den Kreislauf des Saftes in den Pflanzen*, Berl. 1824. *Die Natur der lebendigen Pflanze*, Berl. 1823). This circulation of the cambium is best seen by having a plant of the larger celandine in a pot, and bringing the under-surface of the extremity of a leaf covered with a glass plate under the microscope in a bright light. The vessels follow the divisions of the leaf-ribs. A power of two hundred, with an aplanatic eye-piece where possible, is quite sufficient to bring the phenomenon into view.

subdivision we find all the molluscs, the greater number of the crustaceans and arachnidans, and perhaps the echinodermata.

Vascular System of Invertebrate Animals[225].

§ 110. The simplest form of a circulation of fluids occurs undoubtedly in POLYPES, MEDUSÆ, and WORMS; in INFUSORIES the vascular system is not yet known. In the common polype, the simple stomach or general cavity of the body is prolonged into the arms, and the chyme permeates the canals so formed, being carried towards the periphery by cilia disposed along one side of the canals, and acting in this direction, and returned again to the general cavity of the stomach by cilia disposed along the opposite side of the canals and acting towards the centre[226]. In other polypes, where the stomach and intestine are shut off from the common cavity of the body, the chyle-corpuscles can be seen carried along the internal parietes of the body to the extreme ends of the feathery arms, where they turn round and begin to make their way back again, the motion being effected by the action of the cilia with which the whole inner aspect of the animal is thickly beset[227]. The same thing precisely takes place in many medusæ, in which the chyle is distributed from the stomach in radiated canals to a marginal vessel, from whence it returns to the stomach by the same channels

[225] It is very interesting to observe that the various researches yet made into the structure of the entire division of radiated animals or zoophites of Cuvier, with the single exception perhaps of the echinodermata,—though this is very doubtful,—have not discovered anything like a pulsating heart. All the later accessions to our knowledge assure us that the possession of a circulating system of extreme simplicity unites these into a single natural group. The vascular system here, in fact, bears an affinity in many respects to that of vegetables, but it differs from this essentially in the presence of cilia; it forms a distinct link of transition, however, to the circulating system of the higher animals. The above description is principally after my own observations instituted at Nice in the autumn of 1839; for iconographic illustrations of the subject I beg to refer to my *Icones Zootomicæ*, Tabs. xxxiv. and xxxv.

[226] "The intestinal tubes in the arms with oscillating chyle" are figured by Ehrenberg in the Hydra vulgaris aurantiaca, see his tract:—The fossile infusoria, &c. (*Die fossilen Infusorien und die lebendigen Damonerde*, Berlin, 1837).

[227] The circulation effected by ciliary motions is very beautifully seen in the ciliated prehensile arms of Veretillum, (vide *Icones Zootom.*, Tab. xxxv.)

through which it had come ; the vessels are canals without contractile parietes, but covered with active cilia, and the globules of the chyle are seen moved outwards from the stomach towards the marginal vessel which runs along the one side, and from the marginal vessel inwards, or towards the stomach along the other side[228]. In the planaria and trematoda longitudinal trunks have been observed which subdivide or ramify, and in which under the influence of ciliary movements the blood or chyle is carried hither and thither[229]. In the whole of the classes of animals mentioned, neither vessels with contractile parietes nor hearts have been discovered; cilia alone appear to be the active instruments of the circulation that takes place in their bodies.

§ 111. INSECTS have a contractile heart consisting of numerous cavities, surrounded by sundry layers of muscular fibres. This heart takes up the chyle that is bathing all the viscera, through certain lateral slits or openings guarded with valves, forces the fluid on from chamber to chamber, and finally transmits it into a simple arterial trunk; this aorta, however, does not run far, but again sheds its contents abroad under the brain, from whence they make their way between the tracheæ, muscles, &c., penetrating every part of the body, even to the finest points of the antennæ and joints of the extremities[230].

228 I observed the entire course of the nutritive fluid from the stomach to the marginal vessel, and from the marginal vessel back into the stomach, with peculiar distinctness in a species of medusa belonging to the family of the Oceanidæ at Nice in 1839.

229 This is the system of circulation that exists in Diplozoen paradoxum, and in the distomata and planaria, according to Nordmann, Ehrenberg, and others. (Vide on this point my *Elements of Comparative Anatomy*, § 115).

230 Whether or not this be the universal structure of the vascular or circulating system in the class of insects is not certainly known. The remarkable form of circulating system, however, that is so common in the class, seems to be in relation with the peculiar disposition of the respiratory apparatus which we here observe: the air penetrates by tracheæ into every part of the body of the insect, and there was, therefore, no occasion for a system consisting of tubes, first to conduct the nutritive fluid on all sides for the supply of the economy, and then to carry it for the purpose of aeration to a special respiratory apparatus. The best subjects for showing the dorsal vessel in are perhaps the water-beetles—Ditiscus, Hydrophilus. To obtain a general microscopic view of the circulation

§ 112. In the ANNELIDANS and higher CRUSTACEANS, in all MOLLUSCS, and perhaps in the ECHINODERMIDANS, we find a closed vascular system with superadded pulsatory longitudinal trunks, or true hearts divided into chambers. The annelidans have for the most part a blood-red coloured chyle as their circulating fluid ; the colour here, however, is not connected with the corpuscles, but with the liquid itself ; several highly contractile and rhythmically contracting longitudinal vessels perform the office of heart. The Crustacea have, as a general rule, an aortal heart, which receives from the bronchial vessels for re-distribution to the system the chyle that had been transmitted to them from the systemic veins. These veins seem here to have the duty attached to them of taking up the fresh nutriment or chyle prepared by the digestive system. In the acephalous and gasetropodous molluscs we find either a simple unilocular or a bilocular muscular heart, consisting of an atrium or auricle, and a ventricle, placed between the respiratory apparatus and the systemic vessels, and therefore representing the left or aortal heart of man and vertebral animals generally. In the cephalopoda, again, there are several highly muscular hearts connected with various parts of the vascular system ; two distinct branchial hearts, for instance, each composed of an atrium and a ventricle, transmit the chyle which they receive from the systemic veins and the intestinal canal to the branchiæ, from whence the colourless circulating fluid is brought by the branchial veins to a simple muscular aortal heart of considerable power, and by this is distributed to the system at large[231].

of insects, there is no better subject than the larva of the Ephemera, which is to be had in abundance the whole year through, in every pool of standing water. A form of vascular system similar to that of insects appears to exist in the tracheal Arachnidans, in the Scolopendra, and in a number of Crustaceans (Daphnia for example) but always with modifications. (Vide for further details, my *Elements of Comp. Anat.* § 124.)

[231] The view just given differs widely from those that are most current upon this subject. But if the circulating fluid and its component elements be compared in the animals just mentioned with the chyle and lymph of the more perfect vertebrate series, the greatest similarity will be observed between them ; whilst, on the contrary, no kind of analogy to the true blood will be discovered. The form, size, colour and structure of the corpuscle of the circulating fluid of the backboneless animal, agree in all particulars with the lymph and chyle-

Elements of the Vascular System of Man and the Vertebrata.

§ 113. The vascular system of all vertebral animals is formed after a common type, which is always analogous to that which we observe in man. However different at first sight the structure of the heart and of the larger elements of the vascular system may appear, even as striking is the similarity in all the essential portions of the circulatory apparatus; they are virtually the same in fishes and in mammals. The apparatus which circulates the blood in the vertebrate series of animals consists of the following divisions: 1. Contractile muscular sac-like organs, HEARTS, which as a general rule are associated into a single *central organ* that receives the blood returning towards it from the body and lungs, and sending forth this blood to the body and lungs again; in some few instances, however, we find additional or *peripheral hearts*, hearts appended to particular divisions of the vascular system, for the purpose of urging on the fluids; to this class belong the lymphatic hearts of the amphibia, and the caudal heart of the eel. 2. Elastic tubes, proceeding from or terminating in the central organ and branching throughout the body, or some one of its organs in particular. The vessels which conduct the blood away from the central organ are the *arteries*, those that bring it back are the veins with which must be classed the *lacteals* and *lymphatics*. 3. *Vascular retes* and *convoluted masses*, which belong now to the arteries now to the veins, the branches suddenly dividing into a vast number of minuter twigs, which anastomose freely, and again unite into larger branches,—*retia mirabilia*; or a number of smaller twigs become rolled up together like ravelled skeins, from which simple branches of corresponding size then take their rise,—*glomeruli*. 4. *Capillary vessels,*

corpuscles of the vertebrate animal. The red colour of the circulating fluid in the Annelida is only an apparent analogy, the colour here, as has been said, not being connected with the suspended corpuscles, but with the plasma or vehicle; the corpuscles of the circulating fluid of the Annelidans are colourless, and fashioned in all respects like those of the rest of the invertebrate series. There are, besides, entire families of Annelidans, the Aphroditæ, for example, that have not red but colourless circulating fluids. A farther proof that the circulating fluid of the invertebrata is nothing more than a chyle, exists in the fact, that no one has yet discovered a trace of the lymphatic or lacteal system of vessels in any member of the series.

the reticulations and loopings of various forms, into which the arteries and veins finally resolve themselves, and by which they pass over the one into the other.

§ 114. Anatomy describes the structure of the more conspicuous sub-divisions and elements of the vascular system, the ultimate organization of which is the same in man and all the mammalia. An extremely smooth and transparent membrane, the tunica intima vasorum, composed of an intrication of flat cells, forms a continuous lining for the entire vascular system, clothing the cavities of the heart first, and from this extending through the interiors of the blood-vessels of every description. Strong and peculiarly disposed layers of muscular fibres form the parietes of the heart, and alternately contract and expand its several cavities. The membranous walls of the arteries, veins, and lymphatics, are, in the larger branches of these canals, composed of three layers, the innermost being that which has already been cursorily indicated, and the outermost being merely condensed cellular substance. The middle coat of the vessels differs in the different orders of canals; in the lymphatics and veins it is composed of fine contractile fibres, which appear to be intimately allied to the organic muscular fibre; in the arteries the middle tunic consists of thick but somewhat readily lacerable annular fibres, disposed in several layers, and of the nature of the elastic tissue. Arteries, veins, lymphatics, and lacteals, reduced to their simplest expression, are tubular canals which serve as media for transporting the juices of the body from the periphery to the centre, or from the centre to all parts of the periphery.

§ 115. In the distinctly tubular portions of the vascular system, and before these resolve themselves into their more delicate peripheral and terminal expansions, which we denominate capillaries, the *reté* and *glomerulus* occasionally present themselves. An artery or a vein, to wit, suddenly divides tuftwise into a multitude of fine branches, which form meshes together, and then either lose themselves in the peripheral capillary net-work, or collect again into a trunk of the same calibre as before, which proceeds to its ulterior destination. To this last class belong the lymph and chyle glands, which are universally present and numerous in man and the mammalia, which also occur in birds, though more sparingly, but which seem to be entirely wanting in amphibia and fishes. The lymphatic

glands are condensed retes of the vessels in the course of which they present themselves, spun round with blood-vessels. Retes and retia mirabilia of the arteries and veins are not met with in the human subject: the *helicine arteries* of the penis are the only vessels that seem in part to belong to this category. But in the mammalia they present themselves frequently; arterial retes, for example, occur upon the carotids of the ruminants, and on the principal arteries of the tail and extremities of several different species of mammal, as the Sloth, and the Loris, which are distinguished by the slowness of their movements; also in the orbits of a great number of animals. Retia mirabilia of the greatest extent perhaps of any that exist are encountered in the whale tribe, and also in fishes. Skein-like convoluted masses of vessels, constituting glomeruli, are a general character of the finer sub-divisions of the renal arteries within the cortical substance of the kidneys in man, mammalia, birds, and amphibia. The object of these various arrangements of vessels seems to be to secure a less degree of velocity in the current of the blood, which, indeed, is a necessary consequence of the nature of the structures in question. Whether or not any kind of chemical action takes place in this part of the vascular system is not known.[232]

§ 116. The most important part of the vascular system, with reference to the process of nutrition, is the peripheral, that part which is generally distinguished by the name of the *capillary system*. A

[232] On the occurrence of Retia mirabilia in animals, consult my *Elements of Comparative Anatomy*. Beautiful representations of the extensive vascular plexuses of fishes have been published by Eschricht and Müller, in their tract *On the arterial and venous Retia Mirabilia in the liver of the Tunny, (Thunfisch)*, Berlin, 1836. On the Retia mirabilia of the porpoise, vide Breschet, *Hist. Anat. et Physiol. d'un organ de nature vasculaire decouvert dans les Cetacés*, Paris, 1836, and Baer, in *Nov. Act. Acad. Leopold.* vol. xvii. [There is another purpose secured by the retia mirabilia of some animals, probably of higher vital importance than the ones indicated by the author; this is *to serve as reservoirs of arterial blood.* The spermacæti whale remains for an hour under water without rising once to the surface to breathe; and this it is enabled to do, in all likelihood, in consequence of the large mass of arterial blood which is laid up in the retia that surround the spine in this as in every member of the family of Cetaceans. That the stream of blood suffers a notable retardation in the retia and glomeruli is proclaimed by the recent discovery of cilia within the vascular knots which compose the Malpighian bodies of the kidneys, in some of the lower animals. R. W.]

view of the peripheral capillary vascular system is only to be obtained by the use of fine injections and the aid of the microscope. It is easy to make a collection of finely injected preparations from different parts, and to preserve them, dried or moist, ready for examination[233]. Such preparations serve excellently for demonstra-

[233] Fine injections (in other words the distension of the finest capillaries with coloured matters) have played an important part in physiology for the last century, and have been the means of important discoveries as well as the cause of singular errors. Ruysch (born at the Hague in 1638, died at Amsterdam, 1731) was the first who successfully practised the art of filling the minute capillary vessels with coloured substances, an art which he did not invent, however, but which he learned from his friend Swammerdam. We have numerous figures of his preparations in his *Thesauri Anatomici*, 4to. Amst. 1701—15. His preparations were the subjects of the highest admiration at the time, particularly after Boerhaave had shown himself so much interested with them. Ruysch sold a portion of his collection to Peter the Great of Russia, and another portion to the King of Poland for 20,000 guldens, and this came after his death to Wittenberg. Ruysch's preparations were the immediate cause of the long prevalent error that every part of the body was composed of vascular capillary reticulations. About the middle of the last century, Lieberkühn (born 1711, died 1755) with his fine injections formed an epoch in the art of anatomical preparation-making; and many collections of preparations of his are still in existence in different parts of Europe. Prochaska likewise made many preparations similar to those of Lieberkühn, which are now at Vienna. In the nineteenth century the fine injections of Sœmmerring, Döllinger, Pockels, and Seiler, which were made with variously coloured size or isinglass, obtained great celebrity. In recent times the school of Vienna, in her Berres and Hyrtl, has excelled in the department of minute injections, and has been a sort of manufactory which has now for some time supplied most of the museums of Europe with preparations. The ingredients of the Vienna minute injection are finely levigated cinnabar, copal varnish, and gum mastich; and Berres in his *Microscopic Anatomy*, fol. Vienna, 1837, has given an account of his entire procedure. This work just named contains most beautiful figures of the various forms assumed by the peripheral vascular retes in different parts of the body. E. H. Weber, in his edition of Hildebrand's *Anatomy*, has given figures of the capillary vessels after Lieberkühn, Seiler, and Bleuland. [The terminal arborization of the arteries, and the peripheral relations of the blood-vessels of the different tissues, are depicted in Gerber's *Anatomy*, figs. 122—155. A very excellent means of obtaining minute injections consists in using two saline solutions, which, by double decomposition, give an abundant opaque precipitate. M. Doyere first injects a solution of the chromate of potash till it passes from the arteries into the veins; acetate of lead is then injected, and chromate of lead is precipitated in the minutest capillary vessels. The preparations thus made are said to dry admirably. *Comptes Rendus*, 1841. R. W.]

tion; but they cannot be made the basis of any perfectly satisfactory conclusions, without the term of comparison and means of check supplied by the immediate inspection of the transparent parts of living animals, or of single particles of organs of the recently killed animals, still full of blood[234].

§ 117. However different the more minute capillary reticulations in the various organs appear, they may nevertheless be all reduced to a single fundamental type, a type which is most readily observed in the vascular distribution of the intestinal villi (Fig. CLV.): the terminal twig of an artery (*b*, *b*) bends round into the terminal twig of a vein (*a*, *a*), and the two are repeatedly connected by means of delicate loop-like twigs, these in their turn being formed into meshes by cross or intermediate branches. The fundamental type of the peripheral vascular system is therefore an arterial and a venous branchlet—proper capillary vessels, and an interposed net-

[234] With a little practice in the use of the microscope and some dexterity in manipulating, it is easy to obtain views of the capillary nets still filled with blood-corpuscles, in animals that have been strangled. An examination of this kind is necessary when the business is to conclude in regard to the histological relations of the most minute vessels themselves, as well as of the parenchyma of particular parts.

Fig. CLV.

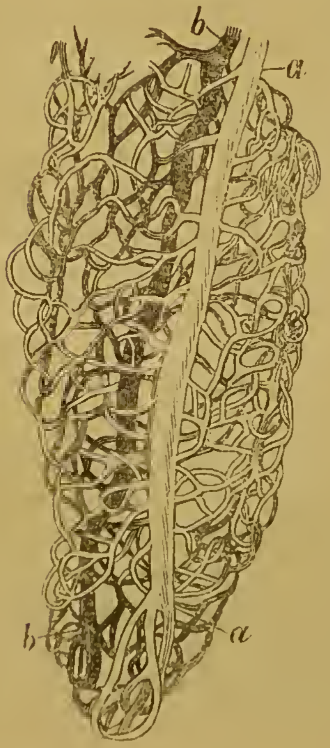


Fig. CLV. Vessels of one of the intestinal villi of the hare; after an extremely beautiful dry preparation by Doellinger. The villus is magnified about 45 times. The vein *a*, *a*, is injected with white; the artery, *b b*, with red; between the two a most beautiful rete of capillaries is apparent. [Compare this with the vessels of the intestinal villi of the horse, Gerber's *Anatomy*, fig. 136. R. W.]

work of fine vascular canals—vasa intermedia[235]. A distinct separation between capillaries, and intermediate vessels, as this is perceived in the intestinal villi more especially, is not generally to be observed, the two blend or are lost insensibly in one another. The parenchyma or organic substance which lies between the finest vascular subdivisions forms islets of very various size and figure, according as the meshes of the intercurrent vessels are opener or closer, and as they are rounded or angular. The intimate structure of every organ, the mode of union and of the grouping of its elementary parts, and the diameter of the vessels which appertain to it, give rise to the greatest diversity of form in the peripheral vascular system, which has nevertheless so determinate a character in each tissue, that an examination with the microscope of the smallest particle of a finely injected preparation enables us to say with certainty from what part of the body it was obtained[236]. The forms of the

[235] The meaning attached to the expression, *capillary vascular system*, has always been somewhat vague. In a general way, the ultimate unions of the arteries and veins have been so called. Berres (*Anat. der Mikroscop. Gebilde*, S. 38) distinguishes the peripheral vascular system into capillaries and intermediate vessels. Among the former he reckons " the most delicate arterial and venous plexuses which, on the one hand, are connected with the more distinct arterial and venous twigs of their system, and which, on the other—and this always with reference to the periphery of the organ under consideration—are in most intimate union, and during life in uninterrupted intercourse, with the intermediate vascular net-work. The structure, the course, and the mode of distribution of these minute vessels still continue true to the general laws of the formation and ramified distribution of the parent vessel. Their plexuses, formed by the manifold divisions and anastomoses that take place, are extremely various, but the majority of them seem to have no other end save that of subdividing and distributing the currents of fluid which they contain." " In the circuit of the intermediate vessels we have a simple, homogeneous, net-like division and combination of the constituent elements, and, at the same time, the most simple form of vascular structure in an anatomical point of view, and peculiar power and activity in harmony with the vital endowment and function of the organ, in a dynamic one."

[236] Sœmmerring first observed the constant relations in regard to form of the elements of the peripheral vascular system; he compared the arteries of the intestines, in their mode of distribution, to the branches of a leafless shrub, those of the placenta he likened to a tassel, those of the muscles to a bundle of twigs, &c. (*De Corp. Human. fabrica*, 1801, vol. iv.) The numerous injections of Berres and Hyrtl of Vienna and Prague, however, first showed the possibility of recognizing each organ by the mode in which its vessels are distributed.

peripheral vascular system have been grouped by several writers into distinct classes, which, however, are not always found observed to the letter, and which are, moreover, rather of anatomical than of physiological importance[237].

§ 118. The forms of the finest peripheral vascular subdivisions appear to be of subordinate consequence in a physiological point of view. The following particulars in connection with this subject deserve specification: 1st. The finest vessels have always distinct parietes; in capillaries of no more than from $\frac{1}{300}$th to $\frac{1}{100}$th of a line in diameter, circular fibres are still to be perceived; but these fibres all disappear in the finest intermediate vessels; here, a simple membrane of great tenacity, and generally structureless—though formed originally from flat cells, and showing their persistent nuclei scattered here and there,—forms the vascular parietes. (Fig. CLVI.) This is to be perceived immediately by the microscopic examination of recent parts, as well as to be demonstrated by the aid of injections[238]. 2nd. The capillary and intermediate

[237] Berres divided the proper capillary vessels into six classes, and the intermediate vessels into three classes—the intermediate mesh-net, the intermediate loop-net, and the intermediate looped mesh-net; and has given masterly delineations of these different forms of vascular distribution. Vide *Mik. Gebilde*, Tab. II. and III.

[238] It is difficult to decide whether the innermost vascular tunic, which, in the

Fig. CLVI.

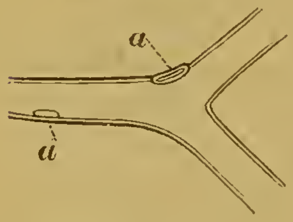


Fig. CLVI. A capillary vessel from the tail of the tadpole. At *a a*, are seen corpuscles connected with the walls of the vessel, which seem to have formerly been the nuclei of cells. After Schwann (*Ueber die Einstimmung*, &c. Tab. iv. fig. ii.)

Fig. CLVII.

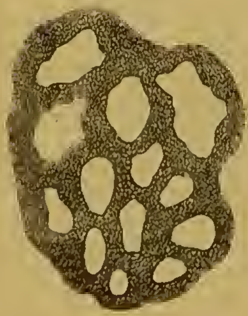


Fig. CLVII. Plan of the formation of the capillary vessels in the area pellucida of the hen's egg; after Schwann, l. c. fig. 12.

vessels which form the meshes or loops have rounded or angular portions of the organic parenchyma inclosed between them, like islets in a river, which differ widely in form in the different tissues. (Figs. CLVII. CLVIII. and CLIX.) In the lungs, these islets are particularly small, and in diameter are often surpassed by the most minute of the vessels; in other parts, again, as in the intestinal villi, for example, (Fig. CLV.), and under the skin in the frog, they are of considerable magnitude. 3rd. The finest vessels

larger blood-vessels, is distinctly seen to be covered with a flattened cellular epithelium, is identical with the simple membrane of the finest peripheral vessels. My observations agree in general with those of Henle (Casper's *Wochenschrift*, No. 21, 1840.)

Fig. CLVIII.

Fig. CLVIII. Incipient formation of vessels in the lamina vasculosa at the edge of the area pellucida of the germinal membrane. From the hen's egg, thirty-six hours after the commencement of incubation. The canals are in some places extremely narrow; where they inosculate they are much wider; the vascular meshes are also very irregular in point of size.

Fig. CLIX.

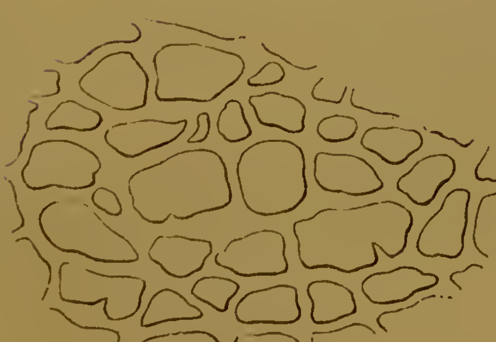


Fig. CLIX. The same object according to Pander, *Entwickelungsgeschichte des bebrüteten Hünchens*, Tab. x. fig. 11.

that are known in the human body are of less diameter than blood-corpuscles, and measure no more than from the $\frac{1}{600}$th to the $\frac{1}{800}$th of a line in diameter; there are consequently vessels—and these are conspicuous enough in the frog—that transmit no blood-corpuscles, nothing but liquor-sanguinis[239]. 4th. The finest intermediate vascular nets do not penetrate the elementary parts of the tissues, but wind about larger or aggregated portions of these. For example, they do not enter into the primary fibres of the muscles and nerves, nor into the constituent parts of the terminal conduits and cæca of the glands; they merely surround these, (vide the Figs. illustrative of the structure of glands under the paragraphs on secretion), and in some places small portions of the cæca are seen as islets between the vessels. 5th. The first formation of the peripheral vascular system in the vitellus exhibits the same opposition and

[239] On this subject see farther on, under the head of Phenomena of the Circulation, § 122: E. H. Weber measured the finest vessels in some of the dried preparations of Lieberkühn, and found the diameters of the smallest to be from the $\frac{1}{300}$th to the $\frac{1}{500}$th of a line; the interspaces, corresponding to the islet of parenchyma, were from six to eight times larger. See his Ed. of Hildebrand's *Anatomy*, vol. III. p. 45. Krause found the diameter of the very finest capillaries of the retina $\frac{1}{540}$th, of the choroid $\frac{1}{01}$st, of the intestinal villi $\frac{1}{555}$th, of the muscular coat of the small intestine $\frac{1}{740}$th, and of the tibialis anticus muscle only $\frac{1}{1110}$th of a Paris line. These extremely fine capillaries, it is to be understood, were not the ordinary ones, which are on an average from the 200th to the 300th of a line in diameter, in relation to which, indeed, they were always present in small proportion, and generally as media of communication between two of larger size; they were, in fact, intermediate or communicating twigs. These numbers agree in the main with the measurements of Berres, Valentin, and myself. Vide Krause's paper in Müller's *Archiv* for 1837, S. 4. [The blood-discs change their form and diameter, when they meet with any obstruction, almost as easily as drops of oil. When the corpuscles pass an unusually narrow space, or impinge on a more solid particle, they instantly become indented, compressed, elongated, twisted, or bent, and recover their usual figure and size with singular rapidity, after passing the obstacle. Indeed, the corpuscles in certain states of disease would even seem to permeate the coats of the capillaries, for the mucous membranes are occasionally covered with blood-corpuscles, when no rent whatever can be discovered by which they could have escaped from the vessels. The extreme minuteness, therefore, of some intermediate vessels is hardly a proof that they would not transmit blood-corpuscles. See Gulliver in Gerber's *Anat.* p. 79, and App. of same, p. 11. R. W.]

relationship between the shut mesh-reticulation of the blood-vessels and the insular and insulated space for the parenchyma of the parent organ in which the vessels take root and spread, (vide Figs. CLVII. CLVIII. and CLIX.)[240]

Phenomena of the Circulation.

§ 119. The entire end and object of the circulation is to convey blood to the periphery of the body, or to the several organs of which it consists, there to furnish elements of nutrition and secretion. The phenomena of the peripheral circulation consequently are those which are of especial importance as regards the peculiar nutritive and secretory processes. The knowledge of the general course of the circulation rests on the basis of purely anatomical facts, and is here presumed to be familiar to the reader. The forces that move the blood, the efficient instruments of the circulation, differ in different divisions of the animal series. They consist of, 1st, Hearts or pulsatory organs in man and the vertebrata universally, and in many invertebrate animals also, insinuated at different places of the vascular system: in man, the mammalia and birds, four muscular chambers—an auricle and a ventricle for the greater

[240] On the formation of the capillary vessels and the primary forms of the retia in the germinal membrane of the bird's egg, consult Figs. CLVII. and CLVIII. where I have given the representations of Schwann, and of Pander and D'Alton, and also of what I have myself seen. Schwann delivers himself in the following terms on the subject of the formation of the blood and capillary vessels. "Among the cells of which the germinal membrane consists, several at certain distances from one another, by lengthening out on different sides into star-like figures, form the primary capillary vascular cells. These elongations of different cells encounter, grow together, the septa between them are removed, and so a network of fine canals of very various diameter is engendered; for the produced portions of the primary cells are much smaller than the bodies of the cells. These prolongations or anastomosing canals of the bodies of the cells, however, enlarge, until they are of equal size one to another, and also to the bodies whence they sprung, consequently until they have formed a network of canaliculi of equal dimensions. The liquor sanguinis is the fluid which was included within the primary as well as the secondary fused capillary vascular cells, and the blood-corpuscles are young cells which are formed within the cavities of the same elementary structures."

or systemic circulation, and an auricle and a ventricle for the lesser or pulmonic circulation—are the efficient instruments in the distribution of the blood; pulsatory organs for propelling the lymph and the chyle are not known in this division (vide § 113). 2nd, Cilia, attached to the inner aspects of the walls of the vessels, the motions of which carry forward the included fluid. These are met with in Polypes, Medusæ, and Worms, § 110; 3rd, of powers that have not been indicated, but of the existence of which we have evidence in the circulation of the sap of vegetables, § 107, et seq. All the older ideas according to which the circulation of the blood in man and the higher animals is accomplished by means other than those just indicated, such as the contractile powers of arteries, the approximation of organs, an inherent motory power in the blood or nutritive fluid, &c., &c., are purely hypothetical. Wherever accurate observations and decisive experiments are possible, there new proof is obtained of the fact that the juices and the blood are distributed by purely mechanical means. It is only as regards vegetables that we are still compelled to betake ourselves to hypothesis [241].

§ 120. It is an invariable and most important circumstance with

[241] As already stated, no one has yet succeeded in showing either pulsatory organs or cilia in vegetables. The simplest form under which the motion of the sap at large takes place is that which is seen in the chara. Here we have hitherto been forced to seek the cause of the motion in the sap itself rather than in the bounding parietes of the canals. [The sorely vexed question of the capillary circulation has been lately approached again by Mr. Martyn Roberts in an ingenious paper *On the Analogy between the phenomena of the Electric and Nervous Influences*, (*Lond. Edinb. and Dublin Philos. Mag.* July 1841). Mr. Roberts is inclined to lay great stress on a neuro-electric influence which he invokes, and which he thinks has the effect of annulling the attraction of cohesion between the liquids and solids,—between the blood and its containing channels; bodies in like states of electrical excitement are known to repel each other; and Mr. Roberts's theory would account for the line of blood-globules which we observe so regularly keeping the centres of the vessels. The best and highest authorities agree, however, in regarding the power of the heart as quite competent to circulate the blood. Still Mr. Roberts's views are ingenious, and supposing them to be well founded, we see that the heart, weaker than it is, would still be adequate to perform its function; the slightest imaginable pressure would suffice to force fluids through tubes between which and them the attraction of cohesion is either greatly reduced or entirely destroyed. R. W.]

regard to the peripheral circulation, to observe, that all the arterial streamlets either turn round and end immediately in veins, or the two orders of vessels, arteries and veins, are in uninterrupted communication with one another by the meshes of an intermediate vascular net-work. This is demonstrated by experiments with fine injections in the dead body, in the course of which the matters are constantly found passing over from the arteries to the veins (§ 116), and by direct observation of the course of the circulation in the transparent parts of living animals. The best subjects for observation are the web of the frog's foot, the tail-fin of a small fish, the membrane of a bat's wing, the gill of the larva of the water-newt, the tail of the tadpole, young embryos of cold-blooded animals, &c. A variety of mechanical expedients, which are soon found out by a little practice, are required for fixing the creatures in making such observations[242].

[242] Cold-blooded animals are by far the best subjects for enjoying the beautiful spectacle of the circulation for a length of time, and without interruption. In what follows I shall say as much as I think necessary to enable every one to undertake such observations most conveniently, and to avoid inflicting needless pain upon the subjects of them—a duty incumbent upon every physiologist, who ought to feel that vivisections are only allowable where they are unavoidable. Every season of the year is not alike favourable for making observations on the circulation. It is only in the spring that tadpoles are to be had, but they are excellent subjects. They should be rolled up in moist blotting-paper, nearly to the end of the tail, and so laid upon a plate of glass of sufficient size, and placed under the microscope, the wrapper of bibulous paper being kept constantly moist by a few drops of water let fall on it from time to time. In this way the circulation may be watched for hours, and the tadpole set free at the end of the observation is nothing the worse. Young and still transparent fishes may also be treated in the same way, and are excellent subjects, but they require more delicate handling than tadpoles. The circulation in the allantois of the young embryos of lizards and snakes is also a very beautiful sight, when these subjects can be had at the proper point of evolution; they require to be removed from the ova, and observed covered with fluid albumen in a watch-glass. In the winter, I find frogs the best subjects; fishes are then much less proper. In the web of the hind foot of the common frog (Rana temporaria), the circulation is perhaps seen to as great advantage as anywhere. All our better microscopes are now provided with a stage adapted for placing the animal, which is best secured by being put into a linen or calico bag, with tapes at each corner to tie it down by. If the stage have a piece of soft wood with a round hole pierced in it, the web is more readily and more advantageously secured over this by being

§. 121. When a transparent part of a cold-blooded animal, the web of the frog's foot, for example, is examined under a low magnifying power, the directions of the arterial and venous currents are readily discovered (Fig. CLX. *a a*, *b b*). The anastomoses of both

pinned down in its circumference, than by threads passed round the toes and braced out in different directions. The web ought of course to be kept constantly wetted with fair water. The mesentery of the frog, or of a small warm-blooded animal, such as a mouse, the wing of the bat, &c. &c., are, on grounds readily conceivable, much less favourable subjects for observation. To obtain a view of the entire embryonic circulation, the incubated hen's egg of the third and fourth day should be chosen. The shell being carefully removed on the lateral aspect of the egg, the germinal membrane must be cut away from the vitellus at the distance of a few lines from the sinus terminalis, and gently placed in a watch glass with a little water warmed to blood heat, and having a few grains of common salt dissolved in it. The adhering particles of the yolk are then to be washed away, the water renewed, the temperature being carefully kept up all the while by the addition at intervals of a drop or two of warm water. To observe the circulation in the respiratory system, the larvæ of the water-newt

Fig. CLX.

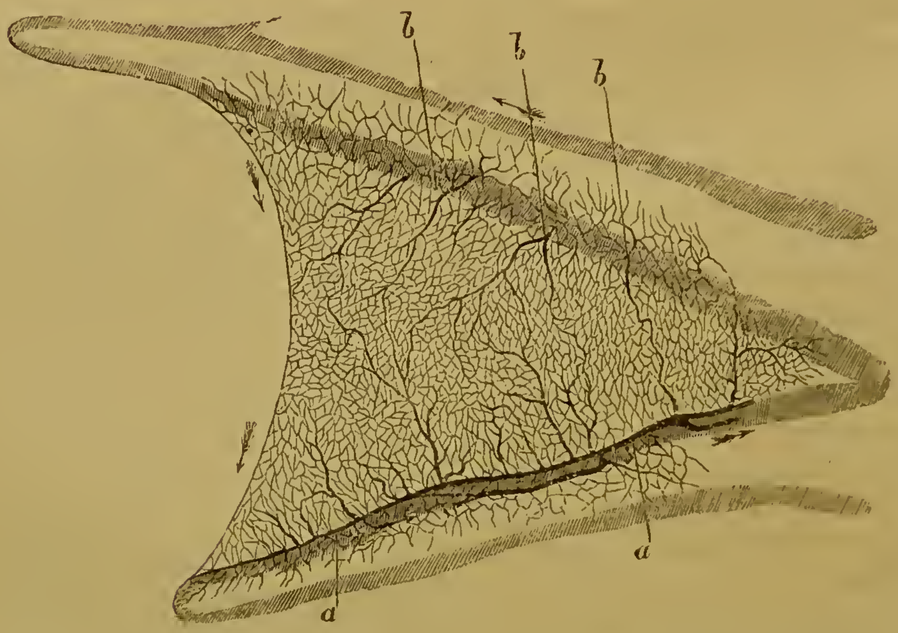


Fig. CLX. Membrane between two of the toes of the frog's (Rana esculenta) hind-foot, with the vessels and their anastomoses, drawn under the lens, and magnified three diameters. *a a*, Veins. *b b*, Arteries.

orders of vessels are seen distinctly. Under a higher power (Fig. CLXI. and CLXII.) a net-work of very fine vessels is perceived lying now over, now under the larger branches, and connected with these by small twigs. In the larger vessels the arterial and venous currents are distinguished, not merely by their opposite directions, but also by the kind of motion appropriate to each: that of the arteries is dis-

may be seleeted to show it as it takes plaee through gills, the branehial fringes being beautifully transparent here. The best subjects for observing the circulation through the lungs—a magnificent spectacle, though it unfortunately lasts for but a short time—are strong, large newts. The animal should be strangled after it has distended its lungs, the noose being pulled with moderate tightness. The abdomen is then to be laid open, and the entire animal being held in the hands, is placed upon a glass plate as a port-objeet, and one of the lungs brought into the field of view. To obtain a sight of the eireulation in glandular organs, the larvæ of water-newts are still the best subjects : to observe that of the liver, in particular, simple lenses, or low powers with aplanatic eye-pieces when the compound mieroscope is used, should be chosen. When we would examine the circulation in transparent parts, magnifying powers of from 100 to 200 diameters are preferable ; but to obtain a satisfactory general view of larger parts, we cannot go beyond a power of from 40 to 50 diameters. To scrutinize individual appearances, we frequently mount to powers magnifying 400 and 500 [and even 800] diameters. Vide fig. CLXIII., in which the web of the frog's foot is represented, this being for all purposes of observation in the direction that engages us the most aceessible and convenient subjects.

Fig. CLXI.

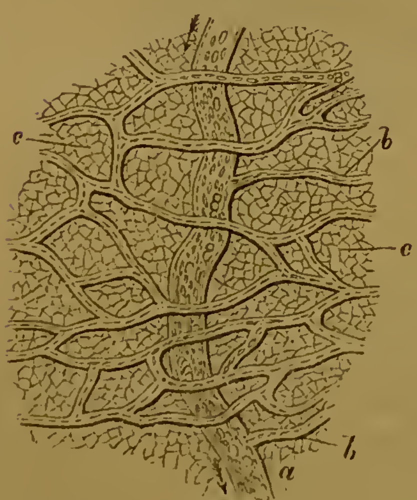


Fig. CLXI. A portion of the web of a frog's foot, exhibiting the included net-work of vessels, magnified 45 times. The angular unnueleated cells *c c*, of the parenchyma, whieh lies between the different vessels, are beautifully shown ; *a*, is a deeper-lying venous trunk, with which two smaller capillary veins, *b b*, communieate. The superficial net-work of eapillaries is seen admitting but a single series of blood-globules. All the vessels here figured are furnished with distinet parietes.

tinctly jerking or pulsatory, but it gets ever less and less, so as the minuter subdivisions are attained, and in the intermediate and finest vessels of all it becomes a continuous stream, which has the character appropriate to the venous current. In all the vessels, even in the very finest, a distinct boundary, formed by a simple dark line, is perceptible ; the surrounding parenchyma, now distinctly cellular, (Fig. CLXI.) now rather granular and fused though still including individual ramified pigmentary cells within it, (Fig. CLXII.) is sharply limited ; the vessels never appear as simple channels pierced through its substance and without distinct parietes. Larger vessels (Fig. CLXII. and CLXIII.) are obviously enough furnished with darker parietes, composed of various layers of fibres. In the most minute

Fig. CLXII.

Fig. CXLII. Vascular rete and circulation of the web of the hind-foot of Rana temporaria, magnified 110 times. The individual cells of the parenchyma are indefinite and obscure. The black spots, some of them star-shaped, are depositions of pigmentary matter. The deep venous trunk, *a*, composed of three principal branches, *b b b*, is covered with a rete of smaller vessels. Mingled with the oval-shaped blood-globules the smaller and rounder lymph-globules are apparent, here, under the blood-globules, there, more on the outside of the stream.

vessels there is room for no more than a single row of blood-corpuscles, and even these can only pass by their long diameters through the axis of the vessel. The larger vessels admit several blood-corpuscles together, and in the decidedly arterial or venous branches, they are observed passing on in all positions—three, four and five abreast, over and near to one another, but those in the centre of the current always in more rapid motion than those on its outside and in contact with the walls of the vessel. (Fig. CLXII. and CLXIII.) Occasionally we observe single vessels of larger calibre running very immediately under the epithelium, which is made up of tabular cells with nuclei, through which the fibrous parietes of the vessel are seen shining (Fig. CLXIII) [243].

§ 122. A magnifying power of from two to three hundred di-

[243] Among the older representations of the circulation in the capillary vessels the best are still those of Reichel : *De Sanguine ejusque motu experimenta*, 4to. Lips, 1767 ; and of Doellinger : *On the Circulation of the Blood*, in *Denkschrift. der Münchner Acad.* Bd. VII. 1818—20. Among those of recent date, the best are probably contained in Dr. Marshall Hall's *Critical and Experimental Essay on the Circulation*, 8vo. Lond. 1831, and in Schultz's *System of the Circulation*, *&c.* Tab. VII.

Fig. CLXIII.

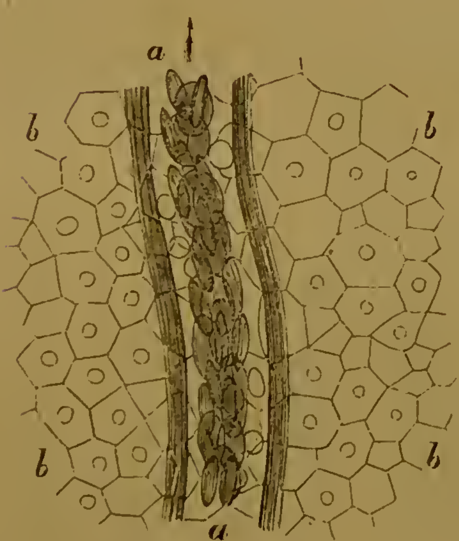


Fig. CLXIII. A venous branch from the web of Rana temporaria magnified 350 times, running immediately under the surface. The cells of the epidermis, *b b b b*, flattened, mostly six-sided, connected like a piece of pavement, and generally provided with nuclei, are seen extended over the vessel. The closely serried column of blood-globules, some with their edges others with their broad faces turned to the eye, is distinguished ; in the clear space betwixt the blood-globules and the parietes of the vessel, which appear made up of longitudinally disposed parallel fibres, the round, clear, and more sluggishly moving lymph-globules are apparent. The object is represented under a weak light.

ameters is required to make out the particular details of the peripheral circulation. The blood in mass or in the larger channels, is seen to flow more rapidly than in the smaller. Here the blood-corpuscles advance with great rapidity, especially in the arteries, and with a whirling motion, and form a closely crowded stream in the middle of the vessel, without ever touching its parietes. With a little attention a narrower and clearer but always very distinct space is seen to remain betwixt the great middle current of blood-corpuscles and the bounding walls of the vessel, in which a few of the lymph-corpuscles (§ 95) are moved onwards, but at a vastly slower rate (Fig. CLXIII and CLXIV)[244]. These round lymph-corpuscles swim in

[244] These clear lymph-spaces were known to the older observers, but were not particularly regarded. In recent times Schultz remarked them, *Circulating Syst.* p. 46, and Poiseuille directed particular attention to them, *Ann. des Sc. Nat.* 1836, p. 3, but they have been more closely studied by E. H. Weber, than by any one else, Müller's *Archiv.* 1837, S. 267. His first conclusion was, that the clear space was bounded by particular walls, each minute blood-vessel being consequently included within a lymph canal; but he soon gave up this idea, which I in my '*Contributions*,' and Ascherson (Müller's *Archiv.*, 1837) have shown to

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Fig. CLXIV.

Fig. CLXIV. View in outline of a large vein of the frog's foot magnified 600 times. The blood-globules, *b* and *c*, present sometimes their thin edges, sometimes their broad surfaces, here they lie parallel, there diagonally, and elsewhere athwart the course of the vessel. The lymph-globules, *a a*, are principally conspicuous in the clear space near the walls of the vessel.

smaller numbers in the transparent liquor sanguinis, and glide slowly, and in general smoothly, though sometimes they advance by fits and starts more rapidly, but with intervening pauses, and as a general rule, at least from ten to twelve times more slowly than the corpuscles of the central stream. The clear space filled with liquor sanguinis and lymph-corpuscles is obvious in all the larger capillary vessels, whether arterial or venous; but it ceases to be apparent in the smaller intermediate vessels, which admit but one or two ranks of blood-corpuscles (Fig. CLXI.) In these vessels the round lymph-corpuscles are seen swimming under, over, and behind the oval blood-discs, both of them proceeding *pari passu* here, and having the same moderated motion : still it is impossible not to observe that the blood-corpuscles are possessed of a greater degree of lubricity, that they evidently glide more readily over one another and over the smooth walls of the vessels, than the lymph-corpuscles, which seem often to get set fast at the bendings of the vessels, and at the angles where

be untenable. [Vide farther on this subject the addition to Annot, p. 292. R.W.] Weber is inclined to view the lymph-corpuscles as products of the degeneration of the blood-corpuscles. He observed that a lengthened stasis of the blood in the vessels was followed by the appearance of lymph-corpuscles in great numbers. The blood-corpuscles stuck to one another and to the walls of the vessels, and rolled over and over in contact with these. They obviously acquired a globular figure from this kind of motion, and the red colouring matter became diffused through the serum, whilst the corpuscles themselves gradually lost their red colour. Weber sometimes saw rolling globules that were distinctly red; he observed other corpuscles that were red and irregular in shape, but that still bore indications of their original form. According to Weber, a stasis of the blood in individual vessels is so common an occurrence, and happens from such slight causes, that it even appears to him to come within the number of normal phenomena, and to have its uses in reference to nutrition. Vide Müller's *Archiv.* 1838. [The breaking up of the blood-corpuscles, here alluded to by Weber, has been lately particularly studied by an excellent English observer, Mr. Quckett, the results of whose observations are, that the corpuscles, when at rest, in a short time become jagged or spinous, first round their margins, and then on their flat surfaces ; the projections thus produced are soon rounded off, and assume the form of globules inclosed within the corpuscles, by which these last acquire the granulated or mulberry appearance so often described. The globules formed in the manner indicated are by and by set free from the containing envelopes, being in some instances sent off with a jerk, in which case they may be seen moving about with a molecular motion ; in others they escape quietly by the margins of the corpuscles, when they continue to adhere to the parent corpuscles. R.W.]

anastomosing branches are received or given off; there they remain sticking for an instant, and then they are suddenly carried on again. Single blood-corpuscles, too, may frequently be observed hurled by a wave, as it were, against angles of the containing vessels, and to remain hanging for a brief interval; at these times they may be seen quivering or oscillating, in spite of the pressure they must undergo; but their stoppages are never long, they soon fly off again, or becoming involved in the general stream they are borne onwards. In contemplating the circulation under these circumstances, a spectacle of the most interesting kind is presented to the eye: the little molecules of the blood are seen in ceaseless motion and alive, but altogether without inherent activity, now borne forward as upon gentle waves, and then pushed more impetuously along; now advancing in serried ranks, now threading their way in single files, the entire phenomena dependent upon the activity of the central organ. In the most minute intermediate vessels of all, a great degree of repose is apparent; single streams are often only recognizable by their bounding parietes; comprehended within two dark lines, these vessels are usually filled with the liquor sanguinis alone; it is at intervals only that a blood-corpuscle, more rarely a lymph-corpuscle, from some neighbouring and larger streamlet detaches itself and makes its way into the canal, which till now had appeared empty; one corpuscle entering in this way is frequently followed by several others in pretty rapid succession, and then, or without anything of the kind occurring, the vessel for a long time circulates nothing but the limpid plasma. Whether there are any vessels or not that never circulate aught but plasma, refusing by reason of the smallness of their diameters at all times to admit the blood-corpuscles, is doubtful[245].

[245] Schultz (loc. cit. p. 169) says: "In the peripheral vascular network of transparent parts, we perceive the greater number of the vessels filled with plasma, in which a larger or smaller number of vesicles (blood-corpuscles) are suspended. These first attract the eye. But besides and between these we soon perceive vessels of greater minuteness, into which no vesicle [blood-corpuscle] enters, their mouths or apertures being of smaller diameter than the blood-discs. These vessels seem to be empty when viewed with a shaded light; but with bright illumination they are found to be permeated by colourless plasma without blood-corpuscles. These vessels I propose to call 'plastic vessels,' by reason of the nature of their contents, and because they are not connected with any serous secretion, but are rather destined for purposes of nutrition." Were the fact as now

§ 123 Such is the peripheral systemic circulation in every tissue susceptible of special examination. In the peripheral vessels of

stated, proved correct, it would be of the highest consequence. But as set forth by Schultz, I cannot assent to its accuracy. I have, it is true, and this especially in the tadpole, more rarely in the adult animal, observed that individual intermediate vessels were so narrow that no blood-corpuscle entered them, lymph-corpuscles only were admitted, and sometimes not even these, or if one or two did penetrate, they seemed to make their way through with the greatest difficulty. From the larger capillaries, we sometimes see transverse twigs sent off, having a broad basis but contracting suddenly, and occasionally appearing to end in blind canals, or to be prolonged into canals of extreme tenuity, which penetrate between the cells of the parenchyma, (something in the manner of Fig. CLVIII). But such vessels are so rare and so dissimilar in form, that I cannot regard them as peculiar vessels. May they perchance be vessels in the course of becoming obliterated, remainders of the primary peripheral vascular system in the embryo? At all events, the subject is deserving of farther inquiry. Were such vessels found to be constant, the plasma would by their means be carried into immediate contact with the minutest elements of the organs and tissues (cells). Two facts seem worthy of being especially considered and investigated: 1. That the most successful fine injections always show a larger number of minute vascular net-works than the immediate observation of the same parts not injected brings to light; 2. That parts which are extremely poor in vessels under ordinary circumstances, become highly vascular in acute inflammations; the sudden appearance of the multitude of sanguiferous vessels that then come to light can neither be explained by supposing a new formation of vessels, nor an enlargement of those that in the usual and normal state are apparent. [In a paper read before the Royal Society in the course of the last Session (1840—41) on the organization and nutrition of parts extravascular and of low-vascularity, Mr. Toynbee has satisfactorily shown that there are many tissues into which, in their state of complete development and perfect health, no vessel penetrates; and that the vessels which anatomists generally had traced to the circumference of such tissues, whence they were supposed to be continued into their substance as serous vessels, actually terminate in veins without the limits of the tissues in question. That the peculiar arrangement of vessels around tissues of low-vascularity as described and figured by Mr. Toynbee, exists, there can be no doubt; but forced injections and pathological conditions, I conceive, show something in addition; I remember when a student myself to have forced fine injections into tissues in which in health no blood-vessel was ever seen, such as the transparent cornea. The force we use with the injecting syringe is often 8 or 10 times that of the heart, and we not only greatly distend those vessels that circulate red blood, but we dilate others that naturally admitted an insufficiency of red particles to make them visible. A vessel with a single row of blood-discs and interspaces about the size of the discs, so far from appearing red, is invisible to the naked eye, at least in mammals. But it might be dis-

every part yet examined, the separation into the quicker stream of blood-corpuscles in the centre, and of the slower one of liquor sanguinis in the circumference above indicated, has been observed.

tended and made conspicuous by an injection; and in inflammation such a minute vessel may and does become turgid and plainly red from the accumulation of blood-corpuscles within it. Proof is yet required of the existence of an order of intermediate vessels which admit only the colourless part of the blood; the blood-corpuscles are so soft and so readily adapt themselves to any kind of minute channel, that they may easily traverse vessels of less diameter than themselves, as noticed in a preceding note. The blood-discs, as such, are obviously unfitted for the immediate purposes of nutrition; yet everything satisfies us that they are the important element in the blood; they are, in fact, stores of nutritive matter, which as they are incessantly produced from the food consumed, so they must be incessantly decompounded and dissolved in the liquor sanguinis to supply the wants of the system. R. W.]

Fig. CLXV.

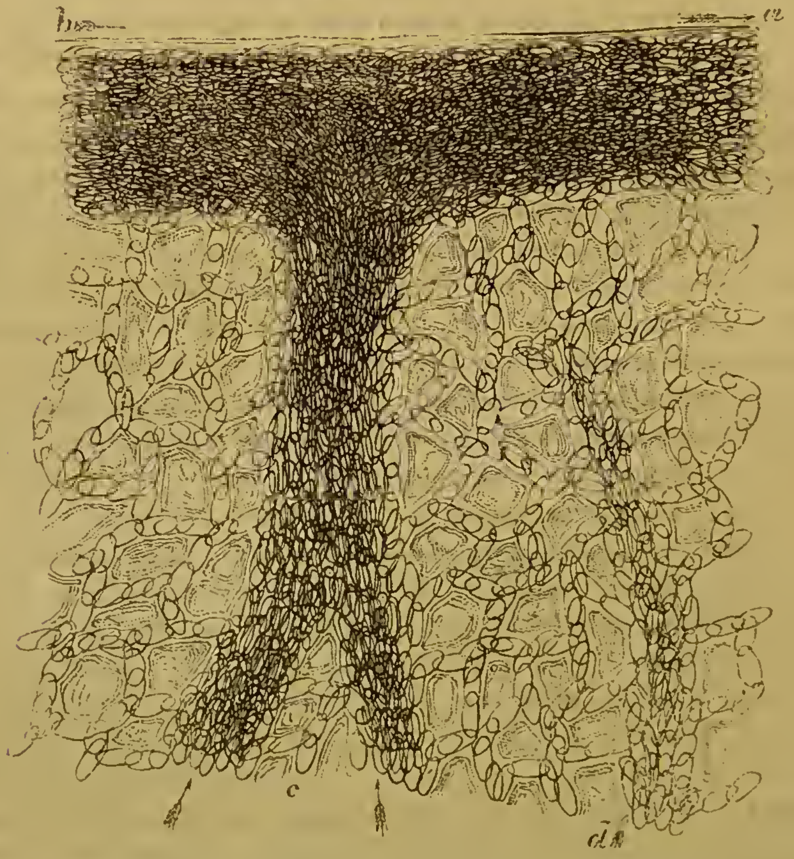

Fig CLXV. Portion of the lung of a live Triton drawn under the microscope and magnified 150 times.

But the circulation of the respiratory apparatus, whether lungs or gills, offers a most remarkable exception to this rule, so uniform in reference to the circulation at large. The capillaries of the respiratory organ are filled with blood generally, *i. e.* liquor sanguinis, with its superadded blood and lymph-corpuscles,—to their very walls. (Fig. CLXV. and CLXVI). It is only in the larger capillary vessels that a thin stratum of plasma is to be seen in contact with the parietes, which are much more delicate than those of the systemic circulation, and not like them formed of a series of dark fibrous layers. The circulation through the lungs of the water-newt is a very beautiful object. The pulmonary arteries here expand very speedily into a fine-meshed net-work of intermediate vessels, which in general admit no more than single files of blood-corpuscles, and play around very minute islets of the parenchyma of the lung. (Fig. CLXVI.) The vessels always appear with distinct parietes, and terminate partly in capillary veins of the same character as themselves, (Fig. CLXV.) partly in larger venous trunks. The blood-corpuscles mixed with lymph-corpuscles (Fig. CLXVI.), as already stated, fill both arteries and veins close to their parietes. The same appearances are presented in the branchial fringes of the larva of the water-newt[246].

[246] This fact with regard to the circulation in the lungs which I was myself the first to observe, I have found confirmed by all my subsequent researches. Vide my *Contributions*, &c., pt. 2, p. 33. Gluge has also noticed that the transparent layer in the stream circulating through a capillary vessel which

FIG. CLXVI.

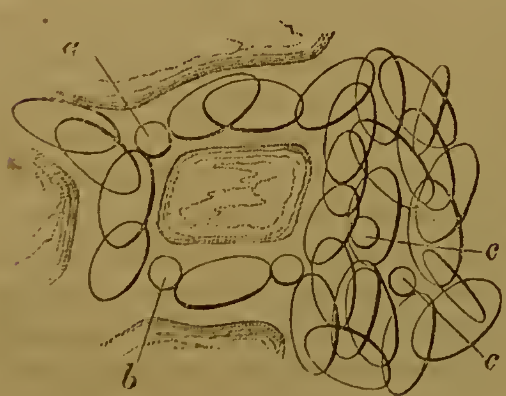

FIG. CLXVI. One of the pulmonary islets bounded by capillaries on three sides, by a larger venous branch on the fourth side. *a b c* are lymph-globules mingled with the blood-globules. The object is magnified about 300 times.

§ 124. The older physiology disseminated a number of erroneous views in regard to the final terminations of the arteries, and the structure of the peripheral vascular system, which still find accredence with practitioners, and even now occasionally make their appearance in pathological writings. Observation recognizes but one kind of termination in reference to an artery—a passage into a vein through a capillary vessel, and an intermediate net-work. All recent inquiry shows that any other termination,—in the secreting canals of glands, in what have been called exhalant vessels, in pores in the parietes of vessels, &c, &c.,—is wholly inadmissible.

§ 125. The most remarkable changes which the blood undergoes take place during its retardation or stasis in the peripheral vascular system. It is whilst the arterial blood is passing through the delicate capillary vessels and the intermediate vascular net-work of the body, namely, that it becomes changed into venous blood. Certain chemical changes then take place that are especially proclaimed to us by a modification in the state of the colouring matter of the blood; but unquestionably other changes are effected at the same time in the state of the constituents of the fluid generally. In the capillary vessels of the lungs, on the contrary, where the blood comes into contact with the air of the atmosphere, the change from dark venous into bright arterial blood is again accomplished. In the secreting organs, again, other changes are effected in the blood, and separations take place from its mass. As a general rule, the peripheral

sometimes measures as much as one-eighth of the diameter of the vessel, is so fine in the lungs of the frog that it scarcely amounts to one half the diameter of a primitive fibre of the cellular substance. *Ann. des Sc. Nat.* vol. xi. p. 60, 1839. [After all, there appears to be no exception in regard to the layer of plasma in the circulation of the lungs; it exists here as elsewhere; it is only smaller in amount. Physiologists seem to have been greatly at a loss for an explanation of the phenomenon; any that has been offered has probably appeared so little satisfactory to the author, that he leaves the point untouched. The views of Mr. Roberts, however, enable us to account for it, at the same time that its existence, though probably not known to him, is strong confirmation of the truth of his conclusions. The blood-corpuscles, as the solid element in the current, are most powerfully repelled by the parietes of the vessel that encloses them on every side, and so they necessarily occupy its centre. On asking Mr Roberts where the blood-corpuscles ought to be found in the circulating mass—congregated in the centre or rolling in the circumference of the stream? he replied: in the centre of the stream. R. W.]

vascular rete here consists of a resolution of the arterial and venous vascular systems. In particular instances, however, in the liver, for instance, the venous blood of the intestines and abdominal viscera generally, collected into the vena portæ, undergoes distribution a second time through a peripheral net-work, which forms combinations with the other vessels that enter and quit the viscus. In the lower vertebrate animals, such as amphibia and fishes, a system of the same kind is encountered in connection with the kidneys.

The whole end and aim of the circulation is therefore to convey the blood to the periphery, that it may there minister to the growth and maintenance of the body, and farther afford elements for the various secretions [247].

§ 126. Many experiments have been instituted with a view to determine the rate of the circulation. The phenomena of absorption (Chapter VI.) afford valuable data from which inferences may be drawn in regard to this point. Experimental inquiry would lead us to conclude that the entire mass of blood must be driven through the body in the space of from one to two minutes, and even less; for in this brief interval of time substances introduced into the stomach are found again in the urine[248].

The motion of the blood, however, has obviously different degrees of rapidity in different parts, according to the structure and calibre of the vessels. The velocity of the blood is greater, for example, in the trunks than in the minute branches, and its rate in the capillaries can even be measured with the eye assisted by the microscope, the length of time which a particular blood-corpuscle requires to traverse a space of ascertained length being easily determined. It

[247] See the Chapter on Respiration and Secretion.

[248] In the experiments of Hering, ferro-cyanate of potash thrown into the veins was found, after very brief intervals of time, in very remote parts of the body; in from twenty-five to thirty seconds, for example, he found this salt in the blood of the jugular vein of the side opposite to that into which it had been injected; in the time mentioned it must therefore have passed through the superior cava, the right half of the heart, the lungs, the left half of the heart, the aorta, the carotids and their capillaries, and the jugular vein; in from fifteen to twenty seconds he found the same salt, which is so easy of recognition, by means of reagents, in the blood of the maxillary artery. After the lapse of a single minute it was detected in the kidney. See his interesting experiments to determine the velocity of the circulation and of secretion, in the third volume of Tiedemann and Treviranus's *Zeitschrift*.

has been found in this way that a blood-corpuscle requires a minute to pass through a space of from twelve to fifteen lines in length, a velocity that is greatly less than we should have been led to expect from the experiments on the absorption of different substances already alluded to[249]. It would seem, therefore, that renewed experiments are wanting to determine the velocity of the circulation with certainty, and particularly to discover the different degrees of velocity that belong to it in different organs and in the different sections of the vascular system.

249 Consult the calculations of Weber in Müller's *Archiv* für 1837, p. 466

CHAPTER III.

OF DIGESTION.

§ 127. The process of digestion includes the whole of the phenomena which are necessary for the formation of fresh blood from the food, from the first assumption of this, to the entrance of the chyle prepared from it into the blood, and the discharge of those parts that are excrementitious. The older physiology divided the digestive process into several acts which bore reference not only to the essence of the process itself, but also included various accessory considerations depending upon the participation of the animal functions. These acts were, 1st, The *prehension* of the food which in the animal kingdom is effected with the jaws, assisted by other instruments appropriate to the purpose—hands, feet, claws, talons, &c. 2nd, The *mastication* or mechanical subdivision of the food by an apparatus contrived for this purpose, generally a chewing apparatus connected with the jaws. 3rd, The *insalivation* of the morsel in the cavity of the mouth. 4th, The *deglutition* or transference of the morsel from the mouth to the pharynx, and its passage from thence to the stomach. 5th, The *chymification* or change of the food into a pultaceous mass called chyme, by means of the chemical process that goes on in the stomach. 6th, The *chylification* or secondary digestion in the small intestines from the moment of the transmission of the chyme from the stomach to that of the passage of the insoluble remainder of the food into the great intes-

tine. 7th, The *excretion* or formation of the excrement during the passage of the insoluble remainder of the food through the great intestine, and its final rejection from the intestinum rectum[250].

§ 128. The whole of the structure and functions of the digestive apparatus are calculated to annihilate the mechanical and chemical qualities of the various articles that are assumed as food from the vegetable and animal kingdoms: the first is effected by means of the masticatory apparatus, and partly also by the motions of the stomach and intestines; the second by the solvent powers of the gastric juice and of the different fluids added to the alimentary mass in the course of the intestinal canal. Whatever is not mechanically made smaller and chemically dissolved, whatever is not reducible from a state of difference to one of indifference, cannot serve as nutriment, and passes either unchanged or unused away, or, in other circumstances, it acts as a mechanical irritant and destroyer; or it proves a poison to the organism, when it is not altered in its noxious properties by the chemical process of digestion, but makes its way unchanged into the blood. In the following sketch we shall take a survey of the morphological relations of the digestive apparatus under a general physiological point of view, and connect the most important organic phenomena of the act of digestion in the course of our survey.

General Morphology of the Apparatus of Digestion.

§ 129. The structure of the digestive system exhibits great diversities in the animal series, which are sometimes connected with the kind of food destined to be consumed, and sometimes, but in a less degree, with the element in which life is passed. The simplest form of digestive apparatus is a tube with an oral and an anal aperture, and a middle enlargement or stomach, or with a single aperture which serves both for mouth and fundament. Among these lower

[250] I shall here consider the subject of digestion in the manner that appears to me most favourable for the comprehension of its essential phenomena, which are apt to be obscured when other circumstances connected with the apparatus of motion are included along with it, these being in fact much more appropriately considered under another head. Neither shall I in this place allude to kinds or classes of alimentary matters, this subject belonging rather to the general and applied physiology, where it will be found discussed and the foundation laid of a physiological system of dietetics.

forms, tubular canals very commonly take their origin from the stomach, and like vessels distribute the chyme immediately to the peripheral parts of the body. In these instances the vascular is obviously not yet distinct from the digestive system. This is the arrangement which we observe in many Medusæ and Polypi, as has been already stated[251], (§ 110.) In other instances, as in the majority of the star-fishes, and in the larvæ of many insects, the oral aperture leads by a short œsophagus into a more or less capacious, membranous, strongly built cæcal stomach, destined occasionally to receive alimentary substances of the hardest and roughest kind, which softens and dissolves the soluble parts, and then by strong contractions returns the insoluble remainder to the oral aperture and expels it[252].

§ 130. In the greater number of the invertebrata, the intestinal canal and its appendages are in all essential respects the same as in the vertebrate series; this is particularly the case in molluscs and insects, but the form and position, as also the prevailing development, are subject to much variety, which, however, is also found recurring in the vertebrata. But there is this remarkable law found dominating the whole of the animal creation, so infinitely varied in point of form, that there is as a general rule a determinate organization and arrangement of the digestive apparatus, typical of the individual classes which compose it. In molluscs, without exception, the liver is enormously developed, and in insects the reverse of this obtains, the liver among them being very small; many organs, such as the spleen and pancreas, are only observed among the vertebrata, and are probably peculiar to them, and so on. But numerous cases occur in which great differences in the structure of the apparatus of digestion are encountered in families of animals which are other-

[251] For specific details upon the subject of this and the immediately succeeding paragraphs, I must refer to my *Elements of Comparative Anatomy*, and *Icones Zootomicæ*.

[252] In the capacious cæcal stomachs of the Actineæ among polypes, and of the Asterias among echinodermata, we often find the remains of animals having shells of the roughest and most pointed description—of different kinds of spinous buccini, of small crustaceans, &c.—which we should imagine could scarcely be taken into the body without injury, and which are nevertheless rejected as empty tenements by and by, the proper animal parts having been completely dissolved out by the sharp juices of the stomach.

wise very closely allied; and then we find ~~now~~ this now that member of the chylopœtic system wanting.

§ 131. As in other particulars of their structure, the vertebrate animals, and especially the mammalia, resemble man in the arrangement and division of the several parts of the digestive apparatus. The principal differences that occur are connected with the kind of food consumed, the purely carnivorous having much simpler and much shorter alimentary canals than the frugivorous tribes. Among the latter, the stomach is not unfrequently compound,—divided into two compartments, as in many of the rodents, or separated into four distinct cavities, as in the ruminants; on the other hand, it is often rounded, and as simple as in the carnivora. It is not, therefore, always possible from the structure of the stomach to infer the nature of the food. The relations of the other portions of the intestinal canal to the quality of the aliment are far more decided and constant than are those of the stomach. In general the length of the intestine is greatest in the ruminants, and stands, in reference to the length of the whole body, in the relation of from 15 to 20 to 1; in the sheep it is even in the proportion of 28 to 1; whilst in the feræ the ratio is usually as 4 to 1, or even, and this is the case among the bats, of 3 to 1. Animals that live on mixed animal and vegetable food, or that can live on food of this kind,—the majority of the rodents, the monkeys, &c., stand in the middle between the two extremes, and it is here that we have the length of the bowel to that of the body in the ratio of 5 or 6 to 1.

In the same way particular parts of the intestinal canal present developments which are often in conspicuous relation with the greater extent of surface, and we may presume of digestive power, required for the assimilation of the vegetable matter which is then the food. The cæcum in all the rodentia and in the horse is very capacious; in the hamster, beaver, hare, &c., it surpasses the stomach itself five or six times and more in size; in the feræ, however, as in the tiger, cat, &c. it is extremely small. Man, from the structure of his teeth and of his stomach, from the length of his intestines to that of his body, (as 6 is to 1,) as also in the very moderate development of his cæcum, seems destined to live on a mixed diet of animal and vegetable substances. And experience both among civilized and uncivilized tribes appears to prove, that a mixed animal

and vegetable regimen is that which is most conducive to the attainment of strength of body, and length of days; although it must be admitted that there are nations which live well on vegetable substances exclusively, and others which live and thrive on a diet as exclusively animal[253].

Structure and Function of the several Digestive Organs.

§ 132. The teeth, which are the essential element in the manducatory apparatus, are subject to great varieties in reference to presence or absence, number, form, position, &c. They are always wanting where, as among suctory insects—flies, butterflies, &c.—fluid aliment only is consumed; among other inferior animals, again, such as the sea-urchin, the crab, and many insects, we meet with an extremely complicated and highly developed dental apparatus, which is often not limited to the jaws, but extends to the stomach, where it also serves to grind and lacerate the food. Among fishes we find sharp, cutting, and blunt teeth of the greatest variety, and in the most multiplied relations; in the pike and trout, for example, we ob-

[253] I pass over all dietetic considerations in this place, catalogues of alimentary substances, poisons, &c. and refer to the general and applied physiology for information on these topics. The appropriate section of Burdach's *Physiology* is very full upon these subjects; but perhaps the most complete treatise on them extant is the third volume of Tiedemann's *Physiology*, which is devoted entirely to the consideration of the appetite of hunger, the instinct to use this kind of food or that, and of the materia alimentaria. Vide also Rudolphi's *Physiology*, vol. ii. part 2. In the elementary works on Physiology that date fifteen or twenty years back, there is a good deal of notice taken of matters from the inorganic kingdom which particular tribes are in the habit of using for a certain length of time as food. In connexion with this fact, the Otomakes and Guemos, tribes of South America, are always particularly mentioned, which, according to Humboldt's account, live during the rainy season, when other food is scarce, upon a kind of clayey earth, and even at other times are in the habit of using a certain portion of the same substance with their food. The fact loses its attribute of extraordinary and incomprehensible, since Ehrenberg showed that there are extensive strata in various parts of the earth which consist almost exclusively of infusory animalcules. In the " bergmehl" or mountain meal, which the inhabitants of the parish of Degernæ in Lapland used in 1832 mixed with the bark of the birch and a little flour for making bread, Retzius discovered the remains of no fewer than nineteen different species of infusoria. We may presume that the " rock-butter" of Kyffhäuser in Thuringia, which is spread upon bread and eaten by the quarriers of the place, is of the same essential nature. On the longevity of different nations, see Prichard, *Natural History of Man*, vol. i.

serve all the bones which bound the mouth thickly beset with pointed needle-like teeth; in the voracious shark the teeth are confined to the jaws, but here they are largely developed; in the carp kinds the teeth are wanting in the cavity of the mouth, but they exist in the pharynx; in the sturgeon and various other fishes they are altogether absent. Among the class of birds teeth are wanting; and among mammalia they present the most singular variety in appearance and in aptness for the functions they have to perform, their structure and arrangement, however, being always in accordance with the kind of food of the family or individual in which they are examined, as this is flesh, grass, or grain, soft tuberous roots or hard woody fibres, &c., or as it consists of mixed vegetable and animal matters; sometimes, too, the teeth are entirely wanting, as among the ant-eaters.

§ 133. The most important part of the digestive system is the STOMACH, the central organ, the element that is never absent. This part requires particular consideration. The stomach presents great varieties in its form and constitution in the animal series. The simplest form of stomach is that which is met with in carnivorous or predaceous animals, in the cat-tribe for example, where it is perfectly simple and of a rounded form; in other mammals, rodents in particular, it is divided into two compartments of very dissimilar structure; in other instances it presents itself in three divisions; and in ruminants it forms as many as four separate pouches[254]. So also among birds it is very common to meet with a pro-ventriculus or maw, and a gizzard—a membranous and a fleshy stomach, and often in addition, a crop. In amphibia and fishes, too, we observe, though more rarely, compound stomachs of the same kind; and in insects and molluscs a crop and double stomach seem the prevailing structure. All these varieties of form are connected with particular modes of life and kinds of food; as a general law, it may be laid down that the stomach is most simple where the food consists of easily soluble animal substances, and that it is most complicated where the harder vegetables afford the sustenance. It is to be observed, however, that in every case in which a plurality of stomachs occurs, there is one which in its structure corresponds with the simple stomach of man and so many other animals.

[254] I have given a view of the principal forms of stomach observed among the mammalia in the VIIth Plate of my *Icones Zootomicæ*.

Structure of the Stomach.

§ 134. To examine the more delicate structure of the stomach, the specimen must be taken from the perfectly recent body of one who has died suddenly or by violence; or the fresh stomach of such an animal as the hog, dog, or cat may be selected[255]. On examining

[255] To see the structures here, the thin slices selected for examination should be taken from the stomach by means of the *double-knife* [a knife composed of a couple of delicate lancet-like blades, capable of adjustment at different angles.]

FIG. CLXVII.

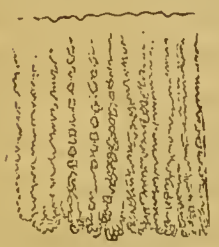

FIG. CLXVII. Gastric glands from the pyloric portion of the stomach, after Bischoff, Müller's *Archiv.* 1838. Tab. xiv. fig. 3.

FIG. CLXVIII.

FIG. CLXVIII. A. Section of a piece of the stomach, not far from the pylorus, with all its elements, to show the gastric glands, magnified about 3 diameters. B. A few of these glands with their racemiform ends, distended with fluid, seen under the compound microscope, and magnified about 20 times.

These glands were examined twelve hours after death, in a female of eighteen years of age, who had drowned herself, all the parts being at the time in a state of complete preservation.

the mucous surface of such a stomach attentively, the whole of it is observed to be covered with little glandular follicles, which open internally; these apertures are surrounded by an abundant vascular net-work, which also extends more deeply and includes the cæcal and somewhat racemiform follicles. The glands are sometimes simple and cylindrical, (Fig. CLXVII.), at others the excretory duct branches repeatedly, and then the glands are truly multilocular or compound (Fig. CLXVIII.) The contents of these glands are always very dark and granular, and their external walls or boundaries of extreme thinness and delicacy, so that the slightest pressure causes them to assume the racemiform structure, and forces out the granular contents. Betwixt these, the secreting glands of the gastric juice, others of a much larger size, and having a more compound racemiform structure, lie singly, filled with completely transparent contents (Fig. CLXXI.); these seem to be destined for a different purpose; they are more common about the pylorus than anywhere else, and deserve a more careful examination than they have yet received[256]. All these glands exist imbedded in the highly vascular

[256] The accounts we have of the structure of these glands vary somewhat; the majority of observers describe the gastric-juice glands as simple follicles, which, according to some, are never racemiform, which according to others are but slightly dilated; I have myself always seen the botryoidal with corresponding

Fig. CLXIX.

Fig. CLXIX. Gastric glands of the Common Fowl; A. Natural size; B. Magnified, after Bischoff, loc. cit. Tab. xiv. fig. 23.

cellular membrane of the stomach; the muscular fibres of the viscus pass clear over them. A slight degree of putrefaction, which occurs so rapidly in the stomach and appears to be so much favoured by many kinds of food, destroys the glands more or less completely; so that their structure, and even their existence is very commonly no longer to be demonstrated very shortly after death; and it is doubtless from this cause that the discovery of these glands is an affair of the very latest times[257].

divisions of the excretory ducts as the normal form in the human subject, and I have thus delineated them in Figures CLXVIII. and CLXX.

[257] In Germany Purkinje (*Bericht der Versammlung deutscher Naturförscher*, &c. 1839,) and Bischoff (Müller's *Archiv*. 1838) have particularly distinguished

Fig. CLXX.

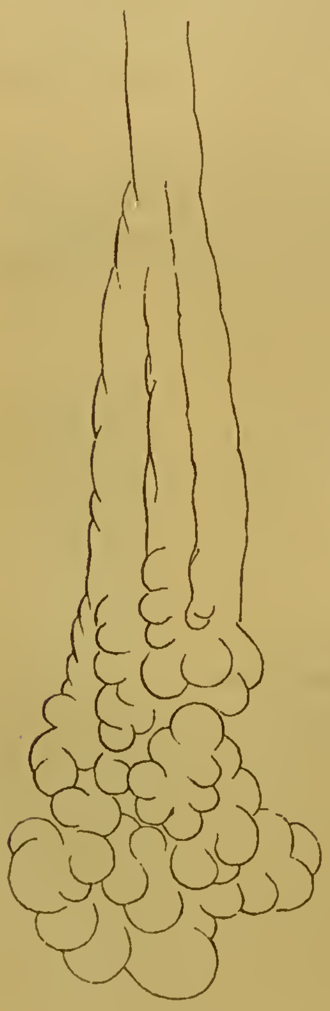

Fig. CLXX. Outline and highly magnified view of the gastric glands from the middle part of the stomach; the excretory duct is composed of three branches which proceed from a multitude of blind cells.

The structure of the stomach in birds is much more easily followed than in animals and man, and is also very important in a comparative point of view. In this class of creatures the glandular layer (Fig. CLXXII, A) lies between the œsophagus (*a*) and the fleshy stomach (*c*); and the gastric glands with their blind extremities turned towards the periphery, are readily recognizable by the

themselves by their researehes into the strueture of the stomach and its seereting glands. The paper of Dr. Sprott Boyd, containing the first announeement of the peeuliar organs in question, is published in the 46th vol. of the *Edinb. Med. and Surg. Journal.* Krause's observations in the "Jahresbericht" to Müller's *Archiv* for the year 1839, also deserve to be referred to; here indeed the whole subjeet may be said to be exhausted,—every point that was erroneous is rectified, all that was wanting is supplied. It were perhaps worth while to examine more particularly than has yet been done the relations of the glands ealled mueous glands, to those that are believed to secrete the gastrie juiee.

Fig. CLXXI.

Fig. CLXXI. Another, probably a mucous, gland of the stomach, from the vicinity of the pylorus, seen under the same magnifying power; it is more eompound in its strueture, and its contents were clearer than those of the gastric glands.

naked eye, shining through the thin superimposed mucous membrane like so many dark bodies, when a stomach which displays them well, such as that of the plover (Fig. CLXXII. A.) is filled with water and viewed against the light. The apertures of the glands upon the inner surface are particularly plain, and the granular contents are voided under the most gentle pressure. These glands are for the most part simple externally; sometimes they form cæcal follicles several lines in length (Fig. CLXXII, B). They are particularly well developed in the gallinaceous tribes, where they are often racemiform and lobular (Fig. CLXXII, B, *e*), or divided in a greater or less degree (Fig. CLXXII, B, *f*); sometimes they are even baccated or like clusters of berries. In young birds the cellular structure of these glands is very conspicuous (Fig. CLXXIII.) and their contents are clearer[258].

[258] For farther details in reference to the structure of the bird's stomach, see my *Icones Zootomicæ*, Tab. xii. The stomach of a fowl or goose is an excellent subject for study, and either of these is most readily procured.

FIG. CLXXII.

A

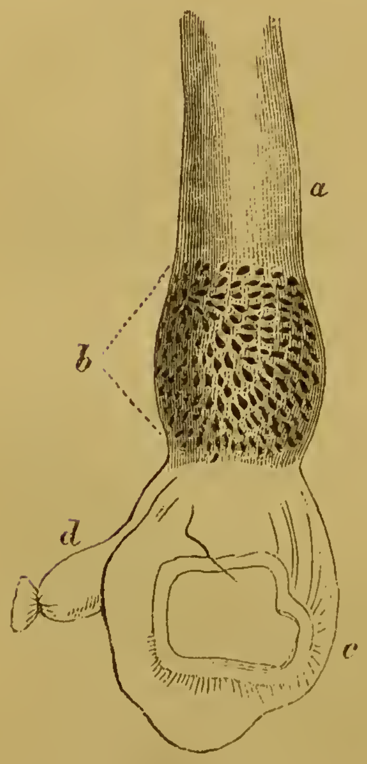

FIG. CLXXII. A. Stomach of the Vanellus cristatus (Common Plover.) *a*, Œsophagus: *b*, Proventriculus, the simple glandular follicles of which are distinctly indicated; some are seen having cleft ends; *c*, Muscular stomach; *d*, Beginning of the duodenum.

§ 135. The relation in which these ventricular glands stand to the production of the gastric juice is not yet thoroughly ascertained. A delicate microscopic analysis of the glands in question shows that their orifices and inner aspects are covered by a fine tessellated epithelium, but that the proper glandular parietes or parenchyma consists of a multitude of minute granular corpuscles, about the $\frac{1}{200}$th of a line in diameter, not always provided with distinct nuclei, but formed of an uniform finely granular mass, rather than of elements having an obvious cellular character. It is in the delicate external wall or envelope of the glands only, that indistinct fibres of cellular tissue can be distinguished ; this part has normally the appearance of a transparent, structureless membrane. The inner surface alone is always covered over more or less completely with a layer of the granules already described, derived from the gland and commonly presenting a membranous consistence[259]. Be-

[259] The first fresh stomach that presents itself will serve for this inquiry—that of a rabbit, or a fowl, for instance. The several microscopical elements of glands and their contents have recently been very particularly examined, and corpuscles and substances of various kinds have been distinguished, without any very clear and comprehensive conclusion, however, having been the result. On this

Fig. CLXXII.

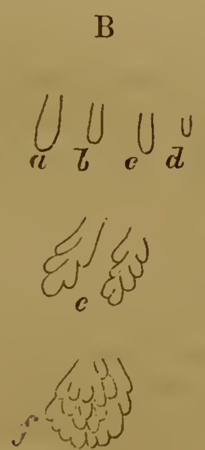

Fig. CLXXII. B Glands of the proventriculus of different birds: *a*, Of the peacock (Pavo cristatus). *b*, Of the Cathartes percnopterus. *c*, Of Casuarius galeatus. *d*, Of Falco pygargus. *e*, Of the fowl. *f*, Of the ostrich. (After Home, *Lect. on Comp. Anat.* ii. pl. 56.)

Fig. CLXXIII.

Fig. CLXXIII. Simple gastric glands of a young Owl : A. natural size ; B. magnified to exhibit the cellular structure of the organs.

sides these granular corpuscles an albuminous fluid is farther found, and in a remarkable case which allowed of the scrutiny being made in the living body, the gastric juice was observed to exude from the surface so copiously upon occasion, that it could be collected in considerable quantity and preserved in bottles for experiment[260].

The gastric juice, indeed, appears to be a fluid loaded with corpuscles, and having a peculiar acid mixed with it, secreted by an appropriate set of glands, from which it is squeezed by the contraction of the muscular fibres of the stomach excited into action by the presence of food[261]. This gastric juice, the existence of which has in very recent times been called in question, but which even older observers knew and admitted, appears to be the sole agent by which the chemical solution of the food is accomplished[262].

topic see the work of Pappenheim, *On Digestion in the healthy and diseased state (Zur Kenntniss der Verdauung in gesunden und krankhaften Zustande*, Bresl. 1839).

260 The highly interesting and important work of Beaumont, *Experiments and Observations on the Gastric juice and the Physiology of Digestion, &c.* 8vo. Boston, 1834; reprinted with notes and additions by And. Comb. M.D. 12mo. Edinburgh), is very full upon this subject. Beaumont's experiments were carried on during seven years in succession upon the same individual,—a Canadian hunter, who was affected with a ventricular fistula, or rather who had a free communication between the interior of the stomach and the outer surface of the thoracic parietes, about two inches below the left breast, the consequence of a severe gunshot wound, but which had not the slightest influence on the man's health, which was excellent. Helm has given an account of a similar case, in which experiments on the changes which the food underwent in the stomach were also instituted—vide his History of two Cases (*Zwei Krankengeschichten*, Wien, 1803).

261 Beaumont observed innumerable points upon the inner surface of the stomach, which presented themselves in the form of fine glistening elevations, covered with a transparent mucus, and apparently ready to burst at the wart-like points, a thin fluid exuding over the entire surface that was visible. This fluid, he goes on to say, is either immediately absorbed by the food when the stomach is full, or it collects in little drops, and trickles down to the most depending part, there to be mixed with whatever happens to be contained in the cavity. This fluid, the efficient agent in digestion, indubitably the true gastric juice of Spallanzani, could be obtained for experiment by mechanically irritating the inner aspect of the stomach, which in the instance in question was done by the introduction of a tube of elastic gum, by which the fluid was at the same time removed.

262 Among the older writings, that of Spallanzani entitled, *Experiments on Digestion*, ought to be held as classical. Spallanzani instituted innumerable

§ 136. It is not true that there is any rise of temperature during the sojourn of the food in the stomach, as was once believed:* and even the mechanical movement of the food in the stomach has much less influence upon its solution than physiologists were formerly disposed to allow, although it is still sufficiently important. When the stomach is distended with food, it alters its position, the great curvature coming forward and tending to rise, by which the regurgitation of the food by the œsophagus is to a certain extent prevented. By the peristaltic motions of the stomach, the alimentary mass is carried from the cardiac orifice towards the pylorus and back again, by which it is brought into contact with every point of the mucous membrane of the organ, and mixed with the gastric juice. The food has been observed, as soon as it entered the stomach by the cardia, to be directed to the left, to descend along the splenic extremity of the viscus, and to proceed along the great curvature towards the pylorus; arrived there, unless sufficiently digested, it is returned by the lesser curvature towards the cardiac orifice, again to recommence the former course towards the pylorus. This generally continues for a few minutes at a time. When the whole of the muscular fibres of the stomach contract, the capacity of the organ is diminished, as a matter of course, and its contents undergo a certain amount of compression. The course or tendency of the contractions, as well as their duration, differs, in conformity apparently with the stimulating qualities of the contents, the healthy or morbid condition of the lining membrane, and according as rest or active exercise is taken after a meal. Everything taken as food is completely mixed together during the process of chymification; and is reduced at length into a homogeneous, pultaceous mass of a faint sickly smell and slightly acid taste—the *chyme*. The colour of this chyme

experiments on mammals, but particularly on birds, and was perfectly well acquainted with the nature and operation of the gastric juice, the existence of which has been denied by several late writers,—by Schulz, for example, in his tract, *De Alimentorum concoctione experimenta nova*, Berol. 1834.

[* Dr. Davy often found the temperature of the stomach as high as that of the heart, and sometimes, though rarely, a degree higher; and the observations of this eminent physiologist dispose him to ask whether the putrefactive process may not be concerned in digestion, according to the earliest theoretical notions on the subject. On the agency of atmospheric air on dead animal matter, &c. in *Physiol. and Anat. Researches*, vol. ii. p. 361 et seq. R.W.]

differs at different times, but less than might have been imagined, according to the kind of food that has been taken; it varies from the yellowish green of cream through different shades of grey. It is frequently thickly pultaceous, but is then no less homogeneous than when it is in smaller quantity and of thinner consistency. It is always uniformly acescent. The chyme which contains a large proportion of butter, oil, or fat of meat, is like thick cream. That which is the product of farinaceous or vegetable food is more like flour-paste or batter.

The escape of the chyme from the stomach takes place in small quantities at once from time to time; in the beginning, or shortly after food has been taken, the discharge goes on more slowly than it does when digestion has made considerable progress; but when the entire mass is chymified, the evacuation proceeds rapidly, and the contractions of the pyloric end of the stomach are rapid and energetic. On an average, food seems to require about an hour to become converted into chyme, so far as to begin entering the duodenum. When the process of chymification is complete, no farther secretion of gastric juice takes place; the stomach becomes quiet, and resumes its former position, until its powers are again called forth by the assumption of a fresh meal. Water and alcohol are not altered by the gastric juice; indeed the same may be said of fluids in general, when they do not contain animal or vegetable nutritive substances in solution or suspension, as, for instance, do soups of all kinds, which must be considered in the light of solid food, requiring to be chymified before they quit the stomach. Simple fluids, on the contrary, soon escape from the stomach,—they sometimes disappear in the course of a few minutes, either absorbed by the parietes of the viscus, or having passed through its pyloric orifice. In proportion as the food is more completely changed into chyme, the acidity of the gastric juice increases notably, a circumstance which is more especially remarkable when the meal has consisted entirely or principally of vegetable substances; the activity of the muscular element of the stomach, especially of the fibres about the pylorus, is at the same time increased, and portions of the digested mass are undoubtedly pressed into the duodenum every time that the mass of chyme is forced up against and closely embraced by the pylorus[263].

263 These details are principally from Beaumont. Many of the facts adduced

§ 137. That portion of the intestinal canal which is comprised between the stomach and the great intestine, the small intestine, the duodenum inclusive, has it in charge to change the chyme into chyle. Much less is known of this process in every one of its elements, in its chemistry, in its functional relations, &c., than of the digestion effected by the stomach. The first division of the small intestine or the duodenum appears to have its own especial function. It is into this part of the bowel that the excretory ducts of the liver and pancreas very uniformly pour their contents; bile and pancreatic juice are therefore here mixed with the chyme. The duodenum is a sufficiently definite portion of the intestinal tract, which has the same structure in mammals as in man, and which in birds almost invariably forms a lengthened loop, within which the pancreas lies. The entire surface of the small intestine is covered with villi, between which there are numerous openings, smaller and larger, which lead to little glands of different forms, and probably of different imports. These are, 1st, *Lieberkühnian glands*, fine, capillary, blind sacs, the openings of which are from $\frac{1}{20}$th to $\frac{1}{30}$th of a line in diameter, so closely placed over the whole of the small intestine that they give the mucous membrane a general sieve-like or perforated appearance. These are probably the secreting organs of the *succus entericus* or intestinal juice (vide § 153); but some have regarded them as the beginnings of lacteals, or at all events have held that they stand in some relation to the function of absorp-

by this observer are also extremely interesting in a pathological point of view, and there are besides many hints well deserving of attention in reference to therapeutics. It is well known how injurious and onerous solid food always proves in acute fevers and in gastric affections. In such cases Beaumont found the mucous membrane of the stomach in a condition corresponding with the fur of the tongue. In slighter febrile affections, whatever their cause, whether in consequence of a chill, of overloading the stomach, of anger, &c., the mucous membrane loses its healthy appearance, becomes red and dry, covered with spots, and so forth. In more severe attacks of the same kind, in which there is simultaneous dryness of the mouth, thirst, accelerated pulse, &c., there is little or absolutely no secretion of the gastric juice, and none is to be had by stimulating the organ in any way. The food will then remain between twenty-four and forty-eight hours in the stomach undigested and unchanged, and cause an aggravation of the symptoms. Fluids, however, are absorbed or carried off with great rapidity; ten minutes after a copious draught not a drop is found in the stomach.

tion. 2nd, The *glands of Brunner*, which are larger lobular and botryoidal glands, $\frac{1}{4}$th of a line and more in magnitude. These glands are observed in greatest numbers in the duodenum, and appear assimilable to that second form of gastric gland which is encountered in the pyloric region in man (§ 134). 3rd, The *solitary glands*, which are simple or but slightly composite follicles, from a quarter of a line to a line in diameter, filled with a granular matter, and which present themselves in greatest numbers in the middle portion of the jejunum. 4th, The *glands of Peyer*, or agminated glands, which present themselves as clusters of rounded glandlets, some quarter of a line in size, and which occur most abundantly in the lower portion of the ileum, more rarely in the jejunum, and are perhaps nothing more than clusters of simple glands. These glands of Peyer seem very susceptible of becoming diseased; they are met with altered in different degrees, in a great number of acute and chronic affections, so that their structure,—which is not yet completely known,—can only be investigated in very fresh bodies of persons in previously perfect health who have died suddenly or by violence. The intimate structure of the whole of the glandular bodies just mentioned craves farther study, and is almost as little known as their individual functions[264].

§ 138. The connection which the villi of the intestines have with chylification and absorption is not known. Various considerations incline us to believe that they play a part in these processes. The villi are highly vascular folds or lappets, covered with a cylinder epithelium, and formed of a delicate indistinctly cellular or granular tissue furnished with an artery and a vein connected by an inter mediate meshed net-work (Fig. CLV.)[265]. Occasionally the distended trunks of lacteal vessels are discovered in the interior of the

[264] The more particular description of these glands belongs to anatomy. The work of Boehm, *De Glandularum intestinalium structura penitiori*, 4to. Berol, 1835, with good plates, and Krause's *Elements of Anatomy*, are worthy of being consulted for information on these bodies; my own observations accord in almost all particulars with those of Krause. I believe the glands of Lieberkühn to be the secreting organs of the intestinal juice. The glands of Peyer are not shut capsules but true secreting mucous follicles.

[265] The work which treats most fully and most satisfactorily on the structure of the villi is that of Henle: *Symbolæ ad anatomiam villorum intestinalium*, Berol. 1837.

villi; this happens both in animals and men who have died or been killed shortly after a copious meal, and when the plexuses of lacteals between the folds of the mesentery are observed replete with chyle. Frequently, especially after milk has been taken, the villi appear turgid, and as if infiltrated with fluid. At the same time, the surface of the mucous membrane of the intestinal canal, generally, is covered with a cream-like substance,—the chyme passing over into chyle, —which in its appearance resembles the chyle of the mesenteric glands[266]. This matter contains a multitude of microscopic granular bodies, which however appear for the major part to belong to the detached and partially altered cells of the epithelial covering of the mucous membrane. Whether the peculiar granular matter which is so constantly found in the chyle is formed in the intestines or is generated and developed in the commencement of the lacteal vessels, is not yet known[267]. But it is worthy of observation, that the intestinal villi exhibit regular and remarkable differences at different periods of life: In the new-born infant and suckling there are mere villous folds in the upper part of the intestinal canal, which as we follow them downwards we see passing into short pyramidal and pointed villi with broad bases. The villi lengthen by de-

[266] In some rare instances we meet with the lacteals of the mesentery in the human subject injected, as it were, with chyle. This occurs most frequently in the bodies of children. The parts of the lacteals which are provided with valves then look like knotty enlargements of the vessels; the villi themselves appear turgid with imbibed chyle. The same thing is more frequently seen in animals, particularly in dogs, which have been fed on milk, or food mixed with butter or fat, and killed an hour or two afterwards. The interior of each villus has then appeared to me to be hollow, and to have a lacteal communicating with it, the vessel appearing as a continuation of the cavity of the villus replete with chyle. According to Krause, a fine, ramified, absorbent vessel takes its origin from the middle of the villi towards their free extremities. Müller's *Archiv* fur 1837, Tab. i. fig. 1.

[267] Granular formations, consisting for the most part of detached epithelial cells more or less altered, are found so copiously mixed with the creamy chyle, that it is difficult to say whether the chyle, which we must presume begins to be formed here, or otherwise the chyme, has any granules peculiar to it. The villi are frequently impacted, as it were, with small, round, oleaginous-looking corpuscles. In the chyle of the lacteals there are numbers of free, very minute molecules, by the aggregation of which the true corpuscles are probably formed. These molecules are so small, that we may suppose them to penetrate through the parietes of the villi.

grees as life advances, and become more cylindrical in manhood. In old age they are distinctly longer than at any previous period, cylindrical, and from their bases onwards of like thickness. The vascular arrangement of the villi is also different at different ages. This remarkable change of form in the intestinal villi is perhaps in relation with the food, and farther, with the condition of the whole process of nutrition at different periods of life[268].

§ 139. During the act of digestion the small intestines appear to be in an incessant state of vermicular motion, by which the chyme is carried onwards. The lacteal vessels meantime absorb the chyle from the chyme, and all insoluble and innutritious matters are moved on to the great intestines, where they begin to acquire the appearance of fæces, an appearance which becomes ever the more distinct the nearer the rectum is approached. It would appear that through the whole course of the great, just as of the small intestines, and particularly in the cæcum, there was an acid fluid secreted by the little glands similar to those of Lieberkühn, which there exist in such numbers, that their closely approximated orifices give the entire mucous membrane the aspect of a sieve. Besides these smaller glands, there are many others of larger size, so that the glandular apparatus here is very abundant.

During the period of digestion gases of different kinds are evolved in variable quantities, from the whole intestinal tract—the stomach, the small, and especially the large intestines. These gases are produced either from the food or from the chemical action of the intestinal juices upon the food. The gases are principally carbonic acid gas, azote, and carburetted and sulphuretted hydrogen. The form, the appearance, and the nature of the fæces change with the quality of the food, and the quantity of bile that is mixed with them. A softish, semipultaceous, brown coloured, and not peculiarly offensive quality of the fæces is that which appears to be normal[269].

[268] These relations, which are known to me in a general way only, deserve a more particular investigation.

[269] On the various points discussed in this section, see § 162, which treats of the chemistry of digestion; the classical inquiries of Tiedemann and Gmelin also deserve to be referred to. Berzelius, so long ago as 1804, undertook the chemical examination of human excrement, *Elements of Chemistry*, 4th ed. vol. ix. 1840, p. 345, in German.) An abundance of crystals, generally of the phosphates of

Glandular Appendages of the Digestive Canal.

§ 140. *Salivary glands.* Great variety is observed in regard to the presence and development of the salivary glands[270]. As a general rule, to which, however, there are many exceptions, it may be said that among animals which live much or altogether in water they are either wanting or but very slightly developed. They are wanting, for example, in the whole class of Cetaceans, in the naked Amphibia (frogs, newts) and in Fishes; in Birds, on the contrary, they are regularly present. Among the Invertebrata the salivary glands commonly present themselves well developed in the shape of a pair or of several pairs of conglomerate glands; in Insects, however, the singular varieties of configuration they exhibit—from the simple salivary vessel, to the compound raceme (vide the Figs. under § 188), excite astonishment. Sometimes the great development of the salivary glands in individual animals is in obvious relation with their mode of life, in the beaver, for example. Still their very common absence shows that they are no very important element in the animal economy. This fact, indeed, has been proved by direct experiment upon man, and is farther shown by the results of artificial digestion. Food of various, almost of all kinds, conveyed immediately into the stomach, or subjected to the action of the artificial digesting fluid, is even as quickly and certainly reduced to the state of chyme as when it is previously mixed with saliva[271]. Insalivation can never with any kind of propriety be designated as a preparatory digestion. The process serves merely to lubricate and soften the food. The salivary glands

magnesia and lime, are met with in feces, as well healthy as diseased; and even in the secreted products of the mucous membrane of the intestines, mixed with bile, as in the meconium of new-born infants and of younger embryos.

[270] The more intimate structure of the salivary glands will be spoken of, and their relations to the other secreting organs discussed, when we come to speak of secretion generally.

[271] This is the result of Beaumont's experiments. When he introduced various articles of food through the fistulous opening of the side into the stomach, he found that if they were but sufficiently comminuted they were changed as rapidly into chyme as when they were introduced in the usual way. Beaumont therefore regards mastication as the most important of the steps preparatory to digestion.

are wanting among animals that live in water, because their food is always penetrated with moisture, and probably very generally swallowed with some of the surrounding medium.

§ 141. The *Liver*. There is one organ which occurs very regularly throughout the animal series, and always in most intimate connection with the digestive canal, this is the LIVER[272]. The general occurrence of the liver is of itself a guarantee for the great importance of the part which it plays in the animal economy. The very constant way in which the product of its secreting function, the bile, is added to the chyme on its entrance into the duodenum, is also a certain indication that this fluid is essential to chylopoœsis, although the way in which it influences this act, and indeed digestion generally, is unfortunately unknown to us; even the chemical constitution of the bile gives no key to its mode of action (vide § 150). On the other hand, however, we know on pathological grounds that disturbances in the formation and excretion of the bile are almost invariably connected with implications of the digestion and nutrition. We in general regard the admixture of the bile with the feces and the coloration of these by the pigmentary matter of the fluid as indicative of a good digestion.

The liver has sometimes been regarded as a simply depurative organ, as freeing the blood from something noxious, and its connection with the intestinal tube, consequently, rather as accidental than necessary, the intestine serving in some sort for its excretory duct. But not only are the pathological states just alluded to declaratory against this, but the evolution of the liver is so likewise. It always appears in the embryo as an organ formed partly by evolution partly by simple growth from the mucous lamina upon the intestine, and always connected with the intestinal tube at the same spot, just behind the stomach[273]. The gall bladder, however, is obvi-

272 On the intimate structure of the liver and its relations, as an organ of secretion, see by and by—§ 195 and 196.

273 [That the liver, in spite of these considerations, is less an organ subservient to chymification than of excretion seems to be proclaimed by the large size of the viscus in the fœtus, when there is no digestion going on; and in a minor degree by the consideration that many persons suffer from weak stomachs all their lives whose biliary system nevertheless had never been affected. The disordered digestion which so constantly accompanies obstructions of the biliary ducts is always complicated by the retention within the body of one of its excretions; the digestion seems to suffer about as much in Anuria as in Icterus. R. W.]

ously of no peculiar importance; in some rare instances it has been found wanting, in consequence of original malformation[274], and in other cases it has been greatly altered by disease, and even completely obliterated without serious effects[275]; among mammals and birds, too, the gall bladder is frequently absent, and this in families nearly allied to one another[276]. During normal or ordinary digestion the bile does not seem to get into the stomach, but it has been seen to enter when food of difficult digestion, and particularly fat meat, had been eaten[277].

§ 142. The *Pancreas* is undoubtedly of much less consequence in the animal economy than the liver. The organ is altogether wanting in the invertebrate series, but it is general in the vertebrate with the exception of a few fishes[278]. It is developed in the same way as the liver, arising by the growth of a blastema opposite this organ at the beginning of the intestinal canal. The influence of the pancreatic juice upon digestion, as well as the significance of the organ which secretes it in the general economy, is unknown (vide § 149.) Even pathological states of the pancreas, which are always very obscure, are without influence in enlightening us as to the purposes it serves[279].

[274] Vide Trott, *De Vesicula fellea*, Erlang. 1822, where the most important pathological facts connected with the gall bladder are collected.

[275] I once saw a case of the kind myself, and others have been frequently observed.

[276] The gall bladder, for instance, is absent in the stag and camel, and not in other ruminants; it is also wanting in the ostrich, in the pigeons, and in the majority of the parrots, though some of them have it.

[277] Beaumont rarely saw bile in the stomach, and only when the use of oily or fat food was continued for a certain time. Fat always remains longest in the stomach, and is chymified with the greatest difficulty, the acid gastric juice obviously attacking it with extreme slowness. Beaumont could not determine, however, whether the entrance of bile into the stomach was a consequence of the indigestibility of fat meats, or took place as a means of assisting the chymification of such articles.

[278] The pancreas seems to be very general among vertebrate animals; even in the bony fishes it is more constant than was at one time supposed, a fact announced by Jo. Müller, and which I have found confirmed in so far as the pike and trout are concerned. It is only in the cyclostomes that it seems to be entirely wanting, an order in which the spleen also exists in a very rudimentary state.

[[279] The pancreas I should imagine to exist as a means of diluting the thickly pultaceous chyme on its escape from the stomach.—We have seen that the stomach is

The function of the *Spleen* is also unknown: it only occurs among vertebrate animals; nor is it even universal among them, for it seems to be wanting in several fishes. That the spleen is of no great importance in the animal economy is demonstrated by the fact, that it may be extirpated without any peculiar ill effects[280]; it also suffers extensive material changes—enlargement, for instance, often to an extraordinary extent, as a consequence of intermittent fever, and yet no particular mischief ensues. In its intimate structure the spleen is singularly vascular, the vessels in their minute subdivisions playing around certain peculiar white corpuscles, the *splenic-corpuscles*, as they have been called. It seems probable that the spleen must have some peculiar or specific influence upon the blood which circulates through it, although what the nature of this may be remains a mystery. The great vascularity of the spleen, though it have no excretory duct, cannot be in vain[281].

§ 143. The chyle, which is formed in the intestines, makes its way into the beginnings of the lacteal vessels by a means not yet perfectly understood (§ 138), and from thence into the absorbents of the me-

a very sieve to watery fluids of all kinds taken into it, none of them remain; their presenee would obviously have interfered with the aetion of the gastrie juiee by diluting it over mueh. They are therefore immediately absorbed into the blood, and only restored to the ehyme by the medium of the panereas in graduated quantity and as it is entering the intestine, when we may presume that a eertain degree of attenuation must be indispensable to the separation of the ehyle from the insoluble and unservieeable residue. R. W.]

280 Aeeording to the experiments of Mayer (*Salzb. Med. Chirurg. Zeit. Jahrg*, 1815, Bd. 3. S. 189) who extirpated the spleen from a half grown male eat; the wound closed on the 16th day; the animal was still alive more than two months afterwards. Dupuytren supposed that he had seen great voraeiousness of appetite follow extirpation of the spleen.

281 The most important works published on the spleen are those of Heusinger, entitled: *On the Structure and Function of the Spleen* (*Ueber den Bau und die Verrichtung der Milz*, 1817.) of Giesker: *Splenology*, Zurieh, 1835, and the paper of Müller, *On the intimate Structure of the Spleen*, *Archiv für Physiologie*, 1834. [I have just alluded to the *pancreas* as the organ by whieh the due and needful dilution of the ehyme was aeeomplished. The situation of the *spleen* and its eonnexion with the stomaeh and the portal eireulation seem to me to give a key to its funetion. The rapid absorption of water by the gastrie veins upon oeeasion, must be aeeompanied by a great degree of attenuation of the blood they eontain, whieh, sent immediately to the liver, would be apt to transude the parenehyma of that organ too freely; but the blood of the spleen, on the other hand, under-

sentery[282]. The course of the chyle is indubitably retarded in the convoluted masses of lymphatic vessels which constitute the mesenteric glands, to the end, in all probability, that some interchange of matters may take place between the blood and the chyle, or that some peculiar influence may be exerted on the newly absorbed fluid. Any influence of this kind, however, cannot be of great importance, seeing that the mesenteric glands, although they exist in the mammalia generally, and often very highly developed, are wanting among birds. After passing through the mesenteric glands, the chyle, mixed with the lymph from the liver, spleen, remaining viscera of the abdomen, and lower part of the body, is poured into the thoracic duct, which, as is familiarly known, terminates in the left subclavian vein, from whence, mixed with the venous blood of the superior vena cava, it immediately enters the right side of the heart, and is then transmitted by the pulmonary artery through the organs of respiration[283].

Physico-chemical part of Digestion.

(BY DR. JULIUS VOGEL.)

§ 144. During digestion the food suffers certain alterations in its

goes a very considerable inspissation,—the absorbents of no organ in the body are comparable to those of the spleen in point of magnitude; the much diluted blood of the gastric veins added to the greatly inspissated blood of the splenic veins composes a fluid of medium density fitted for circulating through the liver. The spleen is, therefore, an appendage to the portal circulation, and its office is to prevent mischief to the liver from the rapid absorption of watery fluids taken into the stomach along with the food, the removal of which fluids is a necessary prelude to the act of digestion. R. W.]

[[282] The entire subject of secretion is exceedingly obscure, it must be allowed, but I do not find any greater difficulty in the penetration of the lacteals and lymphatics by the fluids for which by their inherent constitution they have a peculiar elective affinity, than I find in the penetration of the gall-ducts by the bile, and of the tubuli uriniferi by the urine. The lacteals and lymphatics may be viewed as the essential elements of a kind of universally distributed gland, whose common efferent duct terminates at the angle formed by the junction of the left subclavian with the left jugular vein; the vesicles or tubuli into which all glands resolve themselves, select their appropriate matters from the blood; the lacteals choose theirs from the fluid which is entangled among, and which doubtless permeates the villi of the intestines. R.W.]

[283] The microscopic constitution of the chyle has already been mentioned (p. 97), the general physical and chemical qualities of the fluid will be spoken of by and

physical and chemical properties, the knowledge of which is of great interest and importance in a physiological point of view. A portion of the mass so altered, is absorbed and added to the blood, by which it undergoes farther change; another portion of the mass passes through the intestinal tube without being absorbed, and is finally discharged as excrementitious.

The changes which the food undergoes in the digestive canal are principally effected by certain fluids which are secreted by organs especially destined to this end, and mixed with the food either in the stomach or shortly after its passage from that sac. To give a complete view of the process of digestion, it is therefore necessary to enquire, first, into the physical and chemical qualities of these fluids, and then to pursue the successive alterations which the food undergoes in its passage through the intestinal canal; and lastly, to examine the constitution of the fluid which it is the end of these changes to produce, and which is finally mingled with the blood—the *chyle*[284].

The Fluids concerned in Digestion and Chymification.

The Saliva.

§ 145. The saliva is a clear colourless and somewhat mucous fluid, which is generally alkaline, more rarely neutral or acid in its

by. [According to Mr. Gulliver's observations, the chyle of the mesenteric glands is richer in globules than the chyle of any other part of the lacteal system. See Gerber's *Anat.* Note, p. 57, and *Appendix* to the same, p. 92, figs. 277 and 278. R. W.]

[284] The doctrine of digestion, in recent times, and particularly our knowledge of the processes that take place in the stomach, have been principally advanced by the labours of the inquirers of Germany. As leading works those of Tiedemann and Gmelin—*Digestion from Experiments (Die Verdauung nach Versuchen*, Heidelb. u. Leipz. 1826,*)* of Eberle—the Physiology of digestion after experiments performed on the living body and artificially *(Physiologie der Verdauung nach Versuchen auf natürlichem und künstlichem Wege*, Würzb. 1834), of Beaumont, *Obs. on the Gastric Juice and the Physiclogy of Digestion*, Boston, U. S. 1834; republished with a Commentary, by Dr. A. Combe, 12mo, Edinburgh; of Pappenheim, *On Digestion in the Healthy and Morbid States (Zur Kenntniss*

reaction,[285], and of which the specific gravity varies between 1004 and 1009.[286] Even with the purest saliva we always find mixed a few epithelial cells derived from the cavity of the mouth or from the excretory ducts of the secreting glands. The epithelial cells of the mouth are of the tessellated or pavement-like kind, delicate, round, or elliptical corpuscles from the 40th to the 100th of a line in diameter, with a darker and for the most part elliptical nucleus from the 200th to the 400th of a line in diameter. Besides these epithelial cells it is common to observe other still smaller round corpuscles, from the 200th to the 300th of a line in diameter, which are somewhat darker than these, and when unaltered show nothing like a nucleus in their middle; treated with acetic acid, however, a nucleus makes its appearance, and on close inspection this is seen to be made up of several, generally two or three, smaller granules. These smaller corpuscles belong either to the epithelium of the excretory ducts and canals of the salivary glands, or they are merely modified epithelial cells of the mouth. Besides the two kinds of cells now mentioned, the saliva does not appear to have any proper solid constituents. If a quantity of saliva be collected and allowed to stand for a time in a tall glass some grey flocks sink gradually to the bottom, which consist of the epithelial particles already indicated connected together by a little mucus.

§ 146. The saliva consists principally of water, which indeed constitutes something like ninety-nine hundredths of a given bulk. Its other constituents are animal matters: mucus and epithelial cells, a trace of albumen and cassein, phosphoric fat, animal extractive,

der Verdauung im gesunden und kranken Zustande, Breslau, 1839); of Wasmann, *De Digestione nonnulla*, *Diss. Inaug.* Berl. 1839; finally, some shorter papers by Müller and by Schwann in Müller's *Archiv* für 1836.

285 We have very contradictory accounts of the reaction of saliva upon vegetable colours; repeated experiment, however, has shown that in the great majority of instances it restores the blue colour of reddened litmus paper. Donné maintained that an acid reaction of the saliva was indicative of disturbance of the digestive functions; an hypothesis which has been shown to be untenable by recent experiments.

286 The statements of the specific gravity of the saliva also differ greatly. Some say they have found it from 1080 to 1100—which is obviously too high. Tiedemann and Gmelin found it 1004,3, Mitscherlich between 1006,1 and 1008,8, (*Ueber das Speichel des Menschen in Rust's Magazine*, 1832.) In the horse, Schulz found it 1012,5.

(osmazom) and ptyalin, a matter which has received this name from having first been found in saliva, but which occurs in almost every animal fluid;[287] inorganic matters: sulphate, phosphate and lactate of soda and potash, phosphate and carbonate of lime, chloride of potash and soda, and probably a small admixture of sulpho-cyanogen[288] combined with potash or soda. The whole of these substances, with the exception of the epithelial cells, are held dissolved in the saliva. The quantitative relations of the chief of them in the human saliva, according to Berzelius, are the following:

Water	992,9
Mucus (and Epithelium)	1,4
Salivin or Ptyalin	2,9
Flesh extractive (Osmazome) and lactates .	0,9
Chloride of sodium	1,7
Soda	0,2
	1000,0

The relative proportions of these ingredients, however, are not at all times the same, they vary in different individuals, and in all probability in the saliva of the same individual at different times[289].

287 Ptyalin is a substance which is soluble in water, insoluble in alcohol, and which is not precipitated from its state of solution by the reagents which ordinarily throw down the animal principles from their solutions. The ptyalin of Berzelius, however, differs essentially from that which L. Gmelin discovered; the ptyalin of Gmelin, for instance, is precipitated by infusion of galls and the nitrate of the protoxyde of silver; the ptyalin of Berzelius is not affected by these reagents. Berzelius and Gmelin detected no albumen in saliva, though Bostock and Lassaigne had done so; I myself found a very small quantity of albumen in human saliva, which coagulated with heat. It would seem, nevertheless, that the very minute portion of albumen which exists in saliva at any time may be entirely wanting. The same may be said in regard to the fatty matter which some have found in saliva. Berzelius, in his analysis, says nothing of fat, but Gmelin found a substance of this kind combined with phosphorus—a phosphoriferous fat—in his analyses of saliva. It is not uncommon in examining the saliva microscopically, to discover fat-globules.

288 This presence of sulpho-cyanogen in the saliva is extremely interesting, for in none of the animal fluids save saliva is it known to occur. Treviranus was the first to call attention to its existence; Tiedemann and Gmelin confirmed his discovery; but Berzelius justly remarks, that these experiments require repetition on the great scale, in order to free the mind of everything like doubt.

289 In 1000 parts of human saliva, Tiedemann and Gmelin found 988,1 of

The Gastric Juice.

§ 147. In the fasting state the stomach of men and animals contains a mucous fluid in very small quantity, which either does not redden litmus paper at all, or only reddens it very slightly, and which besides water and mucus contains the organic substances and salts that seem to occur in the animal fluids universally[290]. This fluid is entirely different from the proper gastric juice, which is not met with in the empty stomach, but is only secreted during digestion, or in consequence of some mechanical irritation of the inner surface of the stomach[291]. The secreting organ of the gastric juice is a peculiar glandular apparatus, which even constitutes the greater part of the mucous membrane of the stomach.

The gastric juice is a clear, yellowish fluid, generally mixed with a little mucus, without smell, of a slightly saline but distinctly sour taste, and which shows decided acid reaction. This fluid is slow to putrefy, and even prevents the putrefaction of animal matters. The greater number of solid animal substances are speedily and readily dissolved by it with the assistance of warmth[292].

water, 11,9 of solid residue. In 1000 parts of the saliva, freed from epithelial scales and mucus by filtering, of a man who became affected spontaneously with ptyalism, I found 991,2 water; 4,4 ptyalin, osmazom, fat, and albumen; 4,4 of salts of soda, potash, and lime.

290 The fluid obtained from the stomach of a horse which had fasted long, was found by Tidemann and Gmelin to be turbid, of a pale yellow, only very feebly acid, and of specific gravity 1005,7. In 1000 parts it contained 983,6 water and volatile matter, and 16,4 of residue, consisting of fat, resin, ptyalin, flesh extractive, mucus, some albumen, acetates of potash and soda, sulphates of potash and soda, chlorides of potassium and sodium, phosphate and carbonate of lime, and traces of a magnesian salt. It contained, moreover, a little free acetic acid.

291 The fact of the gastric juice being neutral or acid as it is examined in animals fasting or that have recently eaten, explains the diversities in the statements of the older physiologists with regard to its nature. Tiedemann and Gmelin first showed that the proper gastric juice was only secreted during digestion; they procured it pure by causing animals to swallow pebbles or a quantity of peppercorns, which were found to cause it to be secreted in quantity. Beaumont also found that in the man who was the subject of his experiments, the gastric juice was secreted plentifully under the influence of mechanical stimulation. By such means he procured a quantity of very pure human gastric juice which exhibited the properties mentioned in the text.

292 Microscopic studies of pure gastric juice are still desiderata in physiology;

§ 148. The gastric juice consists chemically of water, a free acid, a few organic particles, and the salts usually encountered in animal fluids. The free acid in the gastric juice of man is hydrochloric acid, in some animals it is butyric acid[293]. The organic constituents are ptyalin, osmazome, mechanically admixed mucus, and a peculiar matter which, in combination with the free acid, forms the proper digesting principle, and which has therefore been designated *pepsin.* Pepsin has not yet been analyzed, its chemical constitution is consequently unknown—we are only familiar with its most remarkable properties. It is soluble in cold water, and is precipitated, probably altered, from its solution by boiling, for it has now lost its solvent powers. It is precipitated from its watery solution by alcohol, by the acids in small quantities, and the greater number of the metallic salts, without the destruction of its digesting properties. It operates in so small a quantity, that even $\frac{1}{60000}$th part added to acidulated water endows the fluid with the digesting faculty[294]. The salts of the gastric juice are, chloride of sodium in

it would not seem to have any peculiar solid matter in its composition; at all events, the artificial digestive fluid, of which mention will immediately be made, and which appears to be almost identical with the gastric juice, is, with the exception of a few indefinite granular particles and fragments of cells, free from all solid ingredients.

293 Prout found no acid except the hydrochloric in the gastric juice, (Berzel. op. cit. p. 206,) Dunglison, in the fresh gastric juice from the living human subject, sent to him by Beaumont for examination, besides free hydrochloric and acetic acid, found phosphate and muriate of potash, soda, magnesia and lime, and an animal matter, which was soluble in cold but insoluble in hot water (therefore probably pepsin). In the acid fluid which a patient affected with stricture of the pylorus used to vomit, I found free acetic acid, which was not only recognizable by the smell, but by this, that the distilled fluid, which reacted strongly acid, having chloride of iron added to it, and then ammonia, exhibited the well-known blood-red colour. [The acid from which the sufferers under one form of dyspepsia endure so much, is the acetic or the lactic acid, or a mixture of the two; I believe that one or other of these acids, and not the hydrochloric acid, is that by the agency of which, and of the pepsin, the solution of the food is accomplished; a certain degree of acidity of stomach is indispensable to digestion. R. W.]

294 Pepsin was discovered and named by Schwann, (Müller's *Archiv*, 1836, S. 90,) but it was not isolated by him. Pappenheim and Wasmann have lately given the method of obtaining it in a state of purity. Of its action we shall have occasion to speak by and by, when considering the changes which the food un-

large quantity, a little chloride of potassium, of ammonium, of calcium and magnesium, sulphates of soda and potash, and sulphate, phosphate, and lactate of lime. The quantity of these salts and of the organic constituents is, however, extremely small; both together do not amount to more than from 1½ to 2 parts in 100 of the gastric juice.

The Pancreatic Juice.

§ 149. The pancreatic juice of man has not yet been examined; we only know the composition of that of animals. According to Tiedemann and Gmelin, who examined the pancreatic juice of living dogs, horses and sheep, it is a clear but slightly opalescent fluid of a bluish-white colour, readily drawn out into strings like white of egg, of a slight saline taste, generally showing acid reaction, although, when the animal from which it is obtained is exhausted, it also reacts weakly alkaline. In the pancreatic juice of a dog they found 8,7, and in that of a sheep from 4 to 5 parts of solid matter in 100 of the fluid. The solid matter consisted of osmazome, a matter which became red under the action of chlorine, and which was only found in the pancreatic fluid of the dog, a large quantity of albumen, a trace of free acid, finally, several salts—lactates, muriates, sulphates, and phosphates of potash and soda, and a little carbonate and phosphate of lime. The pancreatic fluid is consequently distinguished from saliva in the larger quantity of its solid constituents, particularly in its greater proportion of albumen, and in the absence of ptyalin, which is either not present in it at all, or only in very small quantity[295].

dergoes in the stomach. Wasmann maintains that the pure gastric juice contains no organic constituents save pepsin, if we except a very minute quantity of an albuminoid matter. The analysis of Dunglison, already referred to, seems to confirm this conclusion; still Tiedemann and Gmelin found both ptyalin and osmazome in the gastric juice.

[295] Leuret and Lassaigne, *Rech. Physiolog. et Chimiques pour servir à l'histoire de la Digestion*, Paris, 1825,) maintain that the pancreatic fluid and saliva are identical. In 100 parts of the pancreatic juice of a horse they found 99 water, 0,9 osmazome, ptyalin, traces of albumen, mucus, free soda, chloride of sodium, chloride of calcium, and phosphate of lime.

The Bile[296].

§ 150. The bile of man, as obtained from its natural reservoir, the gall bladder, is a clear fluid, of a peculiar musky smell, an extremely bitter taste, and a yellowish-green colour. It is thicker or thinner in different cases, but always heavier than water,—its specific gravity is generally somewhere about 1026.* The bile is commonly neutral—it shows neither acid nor alkaline reaction.

Under the microscope, healthy bile appears as a transparent yellowish fluid, with a few corpuscles of different sizes and indefinite forms suspended in it. These are probably mere deposites from the bile, and do not appear to be essential to its composition[297].

With regard to the chemical composition of the bile the greatest variety of view prevails among the most distinguished chemists, and at the present moment it is not possible to point to any one of these as being absolutely correct. Until this can be done the different statements must be viewed side by side or in succession in an historical series.

§ 151. Until the end of the last century the bile was generally regarded as a kind of soap—a combination of resinous matter and fat with soda. Thenard first called this view in question, and gave another theory of the composition of the bile. According to him,

[296] The literature of the chemical composition of the bile is very extensive. The more important papers will be found referred to by Berzelius and Fromherz. The latest researches we possess are those of Demarcay, (Liebig's *Annalen der Pharmacie*, Bd. 27, S. 270,) who explains a large proportion of the contradictions in pre-existing analyses, but who still leaves some gaps which must needs be filled up, before his own views can be received as irrefragable.

[* Dr. Davy examined the bile of the human subject after death from various causes in the interior of Ceylon; his researches show considerable variation in the specific gravity of the fluid. In a man aged 25, for instance, who had died of intermittent fever, the bile was of specific gravity 1,011; in another, of the same age, dead of the same disease, it was as high as 1,044; and in a third, aged 31, whose skin was yellow, it was even 1,055. In subjects who had died of dysentery it varied between 1,010 and 1,043. In a fatal case of gunshot wound, where the bile was healthy in appearance, its specific gravity was 1,016. *Researches, Anat. and Physiol.* vol. ii. p. 34. R.W.]

[297] The bile contained in the gall-bladder of dead bodies is often white and milky in appearance; this is morbid.

the principal constituents of this fluid are, 1st, A *resinous matter—the resin of the bile*—which gives its distinguishing taste and smell to the fluid, and is soluble in alcohol and the alkalis, but not in water or acids; 2nd, *Picromel*, a substance which has a bitter-sweet taste, and is soluble in water and in alcohol, and which gives to the resinous matter the property of being somewhat soluble in water. Thenard found, farther, in the bile, a peculiar yellow colouring matter, upon which the colour of the fluid depends; also free soda, phosphate and sulphate of soda, chloride of sodium and sulphate of lime. According to him, therefore, the bile is no saponaceous fluid, but a solution of picromel and biliary resin[298]. Chevreul confirmed Thenard's views by new analyses; but he added a new substance to the list of those already known,—*Cholesterin*, or biliary fat—which crystallizes in shining plates, and does not saponify with alkalis.

§ 152. Berzelius, who analysed the bile in a different way, came to different conclusions. He found that the bile, after having been freed from some mucus by filtering, consisted principally of a peculiar substance, which he named *Bilin*. This substance is dyed of a yellowish green by the colouring matter which is mixed with it; it has a bitter, ending in a sweet taste; it dissolves very readily in alcohol and alkalis, with more difficulty in water, and is precipitated by acids from its solution in alkalis. It is always united with a little fat (cholesterine and sebacic acid), which can be removed by means of ether. Besides bilin, Berzelius found some flesh-extractive, chloride of sodium, lactate and carbonate of soda, or the same base uncombined, phosphate of soda and phosphate of lime[299]. Prout analysed the bile by the means used by Berzelius, and came to the same conclusions.

[298] The quantitative composition of the bile, according to Thenard, is the following: in 1000 parts of ox-gall he found 875,6 water, the quantity of which, however, is liable to vary; 30,0 biliary resin; 75,4 picromel; 5,0 colouring matter; 5,0 free soda; 9,0 salts. It must appear strange that in spite of the very considerable proportion of free soda according to this analysis, the bile should not show alkaline reaction; on the contrary, that the smallest drop of free acid should immediately give it the property of reddening litmus paper, a fact which Thenard himself observed.

[299] According to Berzelius, oxgall in 1000 parts consists of: 904,4 water; 80,0 bilin with fat; 3,0 mucus derived from the gall bladder; 7,4 meat-extrac-

§ 153. In a very careful analysis of ox-gall Leopold Gmelin succeeded in separating a much greater number of different substances than any preceding chemist. He distinguished, 1st, A musky smelling substance, on the presence of which the smell of the bile probably depends; 2nd, A variety of fatty substances (cholesterine, oleic acid, margaric acid); 3rd, A peculiar crystallizable azotized acid, which he called cholic acid; 4th, Biliary resin, which agreed in its properties with that obtained by Thenard; 5th, A peculiar matter, which he named Taurin, or Biliary asparagin, crystallizable, containing azote, soluble with difficulty in alcohol, readily soluble in water, and not precipitated from its watery solution by acids, alkalis, and the greater number of the metallic salts; 6th, Picromel; 7th, Yellow colouring matter, both of these last being identical with the substances designated in the same way by Thenard; 8th, Several extractive matters (osmazome, ptyalin, &c.); 9th, Casein, an albuminous matter and mucus; 10th, A variety of salts, viz.; bicarbonate of soda, carbonate of ammonia, acetate of soda, oleate, margarate, cholate, sulphate and phosphate of potash and soda, chloride of sodium and phosphate of lime. According to Gmelin's views picromel, and biliary resin held in solution by this substance, are the principal ingredients of the bile. Fromherz and Gugert, by an analysis of the human bile conducted in the same way, arrived at the same conclusions[300].

§ 154. The striking differences in the conclusions as to the composition of the bile so obvious in these analyses, which could not be supposed to depend on any error, as each was the work of one of the most distinguished chemists of the age, led of necessity to the conclusion that the constituents of the bile are very readily decompoundable, and consequently that according to the method of analysis pursued, various new matters were formed from them; that the

tive, chloride of sodium and lactate of sodium; 4,1 free (or carbonate of?) soda; 1,1 other salts.

[300] The whole of the substances here enumerated were not distinctly indicated and separated in Gmelin's analysis—the ptyalin, the casein, the odorous substance, the salts of the sebacic and cholic acids, for example; the presence of these was only made probable; but this ought not to be brought as a charge of any consequence against the above analysis, these substances only playing a very subordinate part in the constitution of the bile.

greater number of the substances hitherto detected in the bile were not normal constituents of the fluid but newly formed products of the analytic process. Demarcay has proved by his experiments that this is really the case. According to him, the bile, when abstraction is made of a minute quantity of common salt, animal extractive, &c., consists of a peculiar animal substance in combination with soda which is of the nature of an acid, and is accordingly named by him Choleic acid. Picromel, and Berzelius's bilin, are, according to Demarcay, slight modifications of choleic acid. By the action of strong acids choleic acid is decomposed into two new substances, one a non-azotic acid which he calls choloidic acid, and which is identical with the biliary resin of Gmelin and Thenard; another an azotic substance, Gmelin's Taurin. By treatment with alkalis, on the contrary, it is decomposed into Gmelin's cholic acid and ammonia. According to Demarcay the bile is therefore, in fact, as it was believed to be of old, a saponaceous combination of choleic acid with soda, containing salts, a little free and saponified fat, and some extractive matters[301].

[301] Demarcay's conclusions afford a key to the conflicting statements hitherto made in regard to the constitution of the bile. His experiments were repeated by Dumas and Pelouse (*Comptes Rendus*, 1838, 2me Semest. No. 8) and in essentials confirmed. But the French chemists present the formulæ which express the elementary composition of the various products obtained by Demarcay somewhat differently from the original inquirer, which have the effect of rendering the explanation of the decompositions that occur much more difficult than they are according to Demarcay's views. In a new work upon the composition of the bile, which came before me after what precedes was written, Berzelius appears to have thrown a veil over the seeming clearness of the views of Demarcay. He shows that the subject is much more intricate than Demarcay had supposed. The principal results of Berzelius's work, which is not completed in so far as these interest the physiologist, are the following: Fresh ox-gall is a combination of bilin, bilifellic acid, cholic acid, sebacic acid, and gall-green with alkalis, to which must be added gall-fat, extractive matters, and some salts. Bilin is the principal constituent of the bile ; it is identical with Gmelin's gall-sugar, which, however, owes its property of crystallizing to an admixture of acetates. It is very readily decomposed, and by acids is changed into bilifellic acid (a compound of bilin, and an acid, the fellic acid, but which has itself the properties of an acid), fellic acid, cholinic acid (and dyslisin ?) ; by alkalis it is metamorphosed into cholic acid (Cholsäure). Even in the most recent bile that can be obtained, this change of the bilin into the two acids mentioned has taken place partially, and besides bilin it, therefore, always contains bilifellic and

The Intestinal Fluid.

§ 155. The glands which are so plentifully distributed over the whole inner surface of the intestinal canal, secrete a fluid which probably aids in the process of digestion or of chylification. The nature of this fluid and its chemical composition in man are entirely unknown; we are only acquainted with that of the lower animals, and even this has never been examined in a perfectly pure state, but always mixed with food, with gastric juice, pancreatic juice, bile and mucus. Tiedemann and Gmelin analysed the intestinal fluid of several animals; that of the small intestines they found generally slimy; in the upper half of the canal it showed weak acid reaction, lower down it was neutral; besides mucus it contained a large quantity of albumen, casein, and extractive matter, and in the horse, a substance which became red under the action of chlorine, corrosive sublimate, and various salts. The fluid of the cœcum they always found acid in the dog; in the horse, on the contrary, it contained sesquicarbonate of soda, and farther, albumen and casein, ozmazome, ptyalin, some ill smelling resinous matter, and fat. The fluid of the colon in the dog was greenish in colour, pultaceous, very offensive in smell, and consisted of a mixture of intestinal mucus and bile; once it showed acid reaction. In the horse the contents of the colon consisted of brown excrements mixed with a few flocculi of mucus. The filtered fluid obtained from the mass contained albumen or casein, osmazome, ptyalin, a matter which became red under the agency of corrosive sublimate, biliary resin with fat and a fetid matter, and several salts.

Phenomena occurring in the course of Digestion.

Changes which the food undergoes.

§ 156. Until the moment of its arrival in the stomach, the food seems to undergo no essential chemical change. In the mouth it

cholic acid. Demarcay's choleic acid (Choleinsäure) according to Berzelius is a mixture of bilifellic acid, bilin and cholinic acid (Cholinsäure). Let us hope that with the conclusion of these researches of the distinguished Swedish chemist our knowledge of the composition of the bile will have reached a point where it will begin to be available in physiological inquiries, which has never yet been the case.

is merely comminuted, and thereby prepared to yield more readily to the solvent process that is to ensue. It is, indeed, mixed with saliva, which moistens the morsel, makes it to be readily formed into a ball by the motions of the mouth, and fits it, endued with the mucus of the tonsils, to be swallowed. The saliva is also of essential use in dissolving the soluble parts of the food, and so proving the medium between them and the organ of taste;—those parts of the food only that are soluble in the saliva excite sensations of taste. To digestion, properly so called, the saliva contributes nothing; it has been ascertained by direct experiment to be powerless as a solvent of every article of ordinary food[302], and on the contrary, food that had not been incorporated with saliva, if sufficiently comminuted, has been found to be dissolved as completely as that which had been mingled with this fluid[303].

The saliva may indeed effect changes on certain articles of food; it has the faculty, for instance, according to Leuchs, of changing starch into sugar; but it is for too short a time in contact with the food to have any such effect ordinarily;—it accompanies the food into the stomach, it is true, but we may presume that its influence there is overcome by the far more powerful one of the gastric juice[304].

§ 157. It is in the stomach then that the proper digestion of the food begins. So soon as the food, comminuted by mastication, ar-

[302] This is the result of Beaumont's researches. Schwann (*Ueber das Wesen des Verdauungs-processes*, in Müller's *Archiv*, 1836) found that the saliva having an acid added to it, did possess a slight digestive power; but as the saliva contains no free acid it is not worth insisting on.

[303] Artificial digestion, or the solution of articles of ordinary food by means of an artificially prepared fluid (of which more anon) out of the stomach, always succeeds without any admixture of saliva, and Beaumont, as we have already seen, found that food placed immediately in the stomach of the man who was the subject of his experiments, if properly comminuted, was as speedily dissolved as that which was introduced after having been chewed and mixed with saliva.

[304] This observation of Leuchs (Kastner's *Archiv*, 1831) has been confirmed by Schwann; the change, however, only occurs very slowly, and it is easy to obtain conviction that starch or amylaceous food is not turned into sugar by being simply mixed with saliva. I have repeatedly detected unaltered starch by the usual test of iodine, not only in the stomachs of healthy animals, but in the fluids rejected from the stomachs of men under a variety of circumstances.

rives in the stomach, an increased secretion of gastric juice ensues, and this being mixed with the solid ingesta, they are gradually dissolved. Such principles as coagulated albumen, fibrine, and cheese, are gradually softened, the several pieces becoming transparent and gelatinous on their edges, and from thence towards their centres; the same thing happens with organized substances, such as meat and vegetables, which go on losing their organic structure more and more, the farther digestion advances. Meantime gases of different kinds are disengaged[305]. The alternate peristaltic contractions of the parietes of the stomach effect the penetration of the aliment with the gastric juice, and the complete disintegration of the softened and now gelatinous mass. Finally, after the lapse of a few hours the whole of the food is found changed into a homogeneous pap, generally of a whitish colour—the *chyme*. The fluids which are taken into the stomach are, in general, very rapidly absorbed from it, in part unchanged, in part chemically altered[306].

§ 158. The alterations undergone by the food in the stomach are of two kinds: *solution* and *chemical change;* but these are not distinct from one another; they both occur simultaneously, and are effected by the same means. Solution has reference of course to the solid food alone: but many fluids coagulate when taken into the stomach, milk, for example, the casein of which, from its state of fluidity, always becomes solid; fluid albumen is also partly consolidated in the first instance by the juices of the stomach[307]. Almost all the solid alimentary substances are dissolved in the

[305] Magendie and Chevreul analysed the gas from the stomach of a man who died by the hands of justice, and who, two hours before his death, had eaten a quantity of bread and cheese and drunk some wine and water. It consisted in 100 parts of 11,00 oxygen, 14,00 carbonic, and 3,55 hydrogen, and 71,45 azote.

[306] This was ascertained to be the ease by Tiedemann and Gmelin in animals, and by Beaumont in the human subject.

[307] The coagulation of milk that takes place in the stomach is explicable, partly from the action of the free acid it encounters, partly from the peculiar effects of the pepsin; the recent discoveries of Fremy, and the researches of Simon (*Manual of Medical Chemistry*, vol. i, p. 86), which were based on them, render it probable that the coagulation of milk by the mucous membrane of the stomach depends on the property which this last possesses of changing the sugar of milk of the fluid into lactic acid. The coagulation of the fluid albumen ensues from the action of the free acid of the gastric juice; but fluid albumen is not always coagulated in the stomach, a fact which Tiedemann and Gmelin proved.

stomach,—meat, and even bone and cartilage, cheese, vegetables, in a word, food by whatever variety of name designated. A few parts only of our aliment resist the action of the stomach, *e. g.* the woody parts of vegetables, the microscopic cortical cells and spiral vessels of which are generally found unchanged in human feces; the horny tissues, such as cuticle, hair, feathers; the stones, husks and skins of fruits and seeds, which mostly pass through the intestines unaltered.

The particulars of the solution of the alimentary substances have already been given in the preceding paragraph: the individual pieces of the food are softened on their external surfaces, and the softening process penetrates by degrees till their centres are attained, and the entire mass is changed into a homogeneous pap, which is miscible with water into a turbid fluid.

Along with the solution, and in proportion as it is accomplished, the food experiences a change, an alteration of its chemical properties. The changes which the food undergoes in the stomach are as yet but imperfectly known. They extend not only to the solids, but also to the fluids that are consumed as food. A solution of common cane sugar, for example, becomes milk-sugar, and mannite and dextrine are changed in the stomach into the same substance; many of the organic saline bodies, such as the citrate, tartrate, and malate of potash and soda become carbonates of the same bases[308]; starch is said to be changed into grape sugar and gum[309]. Coagulated fibrine dissolved in the stomach has lost its property of spontaneous coagulation; albumen coagulated and dissolved, will not again set [310]

[308] This discovery was lately made by Fremy (*Comptes Rendus*, 1839, Iier Semest. p. 96, 2ieme Semest. p. 46, et 165). The transformation according to Fremy's observations is not only effected in the stomach, but by contact with many of the animal membranes. The same may be said with regard to the transformation of many of the salts of vegetable acids into carbonates.

[309] This was ascertained by Tiedemann and Gmelin (loc. cit. S. 301); what share the saliva has in producing this change (vide § 156) has not yet been ascertained.

[310] All observers are agreed upon this point—Tiedemann and Gmelin, Eberle, Schwann, Pappenheim, Vogel, (Liebig's *Annalen*, 1839, April). Gmelin, Eberle, and Schwann, maintained that albumen was changed into ptyalin and osmazome. I had combated this view myself some time ago (Liebig's *Annalen*, loc. cit.) and have found since then that Berzelius has done so likewise (*Thierchemie*, S. 214.

with heat; gelatine loses its property of forming a jelly, &c. &c.[311]

§ 159. Although almost all the articles used as food are dissolved by the gastric juice, the solution is not effected in regard to all with the same readiness and with the same rapidity. Some kinds of food are much more speedily dissolved than others, and these are said to be *easy of digestion;* some have to remain for a much longer period in the stomach before their solution is completed, and these are *hard of digestion;* a few are absolutely insoluble, and these are *perfectly indigestible.* The determination of the kinds of food that are more easy or more difficult of digestion is not unimportant, for it forms the foundation of Dietetics. Beaumont made excellent use of the rare opportunity he enjoyed of instituting experiments upon this subject, noting upon repeated occasions the interval that elapsed between the time at which food was taken and that at which it was digested and expelled from the stomach. The following are a few of the results of his observations: Stewed tripe and boiled petitoes were found the most digestible kinds of food tried; they had both disappeared from the stomach after the lapse of an hour; roast venison was digested in 1 hour and a half; bread with cold milk in 2 hours; boiled stockfish in 2 hours; hashed meat in 2½ hours; young pork in 2½ hours; wild-goose in 2½ hours; turkey in 2½ hours; oysters in from 2¾ to 3½ hours; roast beef in from 2¾ to 3½ hours; boiled beef in from 3½ to 4½ hours,—mean of ten observations 3¾ hours: salt beef in from 3½ to 5½ hours; recently salted pork in from 3½ to 6 hours,—mean of 10 observations 4½ hours; fresh roast pork in from 3¼ to 4½ hours; roast mutton in from 3 to 4½ hours,—mean of 5 observations 3¾ hours; hard eggs in from 3½ to 5½ hours,—mean of 3 observations about 4 hours; soft boiled eggs (2 observations) in 3 hours; roast sausage in from 3 to 5 hours,—mean of 5 obser-

I found that albumen and fibrine after solution by digesting fluid, contained precisely the same relative proportions of carbon and azote as they did in the unaltered, undigested state.

[311] The examples quoted of chemical transformations in the stomach, are probably the only ones that have been placed by repeated experiments beyond the pale of doubt; still the mode in which the peculiar changes are effected remains a mystery. This point is one of the most important in the entire circle of animal chemistry, but it is at the same time one of the most difficult of comprehension.

vations 3¾ hours; boiled fowl (3 observations) in 4 hours; roast veal in from 3¾ to 5½ hours; mean of 7 observations 4¼ hours; dry bread with coffee or potatoe soup (2 observations) 3¾ hours[312]. Beaumont found farther by direct observation that very copious meals required a longer time for their digestion than moderate or small ones, a fact which is known from daily experience; and that with any indication of disturbance of the stomach, the digestion goes on more slowly than at other times. The temperature of the stomach is not increased during the act of digestion; within the stomach, as in other internal parts of the body, the thermometer was found by Beaumont to mark 100° F.

Theory of Digestion.

Artificial Digestion.

§ 160. By what means, it will now be asked, are the various alterations in the food described in the immediately preceding paragraphs accomplished? Do the walls of the stomach by their contractions grind the food mechanically, or do they by some peculiar inherent power, a vital power, animalize it, making it homogeneous with the body, turning it into chyme? Does the food in the stomach undergo a species of oxydation or fermentation, its own elementary principles working the one on the other under the influence of the vital power, so as mutually to decompound each other, and become transformed to chyme? These, and other questions, the offspring of so many hypotheses, have been imagined, but have never been demonstrated; nay they were even disproved by some of the earlier experiments; and at the present day we are in a condition to say and to prove that the solution and change which the food undergo in the stomach are purely chemical in their nature, and depend on the solvent property which is inherent in the gastric juice. We can now regard the stomach as a reservoir for the food, and at the same time as the organ which secretes the solvent liquid, and

[312] These different kinds of food were eaten with bread or vegetables. As the experiments were instituted on a single individual, the conclusions from them cannot of course be held as possessing any claims to be considered as universally applicable; they nevertheless form a very valuable contribution to our knowledge of the relative digestibility of different articles of food in general use.

see its contractions as the mechanical means for securing the due admixture of the gastric juice with the food, and of propelling the mass when properly acted on into the intestines; beyond this the stomach has nothing to do with digestion [313]. An artificial gastric juice can be composed by steeping the mucous membrane of a recent or dried stomach in water rendered slightly sour by the addition of an acid, at a moderate temperature, which will digest animal and vegetable substances,—which will soften and dissolve and chemically alter the articles that form the staple of ordinary food, precisely as the stomach of a living man or animal would do [314]. This is what is

[313] Reaumur, Spallanzani, (*Experiences sur la Digestion*) and Stevens (*De Alimentorum concoctione, Edinb.* 1777) showed that the walls of the stomach contributed nothing of themselves to digestion, but that the gastric juice was the sole means by which the food was dissolved. They performed many experiments both on men and animals, the general and common feature of which was that various articles of food were inclosed in small spheres or boxes perforated with holes and swallowed. It was obvious that the pressure of the coats of the stomach could contribute nothing to the digestion here; nevertheless, when the spheres were passed by stool, they were always found empty, their contents having been dissolved out of them. Boerhaave held digestion to consist in a kind of fermentation, an idea that has long since been abandoned. The proposition of C. H. Schulz, that there is no such thing as a peculiar gastric juice, but that the fluid so designated is a product of the digestive act itself, has been satisfactorily gainsaid by the direct experiments of Tiedemann and Gmelin, and of Beaumont, who procured the proper gastric juice by exciting the stomach mechanically, and used it with effect for dissolving various articles of food.

[314] The statement that digestion is a purely chemical process may perhaps appear questionable to some; but there can nevertheless be no doubt of the fact. The power that calls an organized being into existence, and maintains it in activity during the term of its life, lies beyond the province of chemistry, indeed; and no rational chemist will ever think of producing a plant or an animal by any chemical process; but the products of the vital processes, abstracted from their form and regarded in their materiality only, fall completely within the domain of chemistry. When preserved from decomposition, they retain their properties long after the death of the organism which engendered them; and like other organic and inorganic substances, they undergo determinate changes when brought into contact with different reagents, which always occur in conformity with the same laws. These changes are, with perfect propriety, placed in the domain of chemistry. The existence of one or more powers, commonly called *vital powers*, is not, however, denied when this is done. The final cause of the secretion of the gastric juice lies in the nature of the animal organism, and is unknown to us; but the effects of the gastric juice, once it is formed, upon

spoken of as *artificial digestion, artificial chymification:* by its means we are enabled to institute much more accurate experiments on the changes which the food suffers, than we should ever find occasion to make in the course of the natural digestion in the living body; many of the admitted facts in connection with the subject of digestion have been derived from experiments on the process carried on artificially[315].

the food, is a purely chemical process, which will go on out of the stomach in any ordinary vessel. From a *dried* stomach, in which assuredly there is no inherent vital power, we can prepare as efficient a digesting fluid as from a fresh one.

[315] A good deal has already been written on artificial digestion, the discoverer of which was Eberle (loc. cit.); Müller and Schwann pursued the discovery farther (Müller's *Archiv*, 1836), and additional contributions to our knowledge were subsequently brought by Pappenheim (loc. cit.), and by Wasmann in his dissertation. In instituting experiments on artificial digestion, the best procedure is the following: The fresh and clean-washed or the dried stomach of an animal,—if it be that of a ruminant the fourth stomach or rennet must be selected,—turned inside out, is put to soak in from one to two quarts of lukewarm water, to which so much of an acid, and the best is perhaps the hydrochloric, has been added as to make it taste pretty sharply sour, without however attacking the teeth. The stomach is digested with this fluid in a temperature of between 90° and 100° F. during from 6 to 12 hours, and then the liquor is poured off; this is the artificial gastric juice, which serves perfectly for experiments in a general way; but if the purpose be to examine the products of the digestive process very particularly, it is proper to have a purer and more carefully prepared fluid. Wasmann recommends us to separate the mucous membrane of the middle parts of the stomach from those that surround both the cardia and pylorus, this, according to him, containing a larger quantity of pepsin than these. The part of the membrane selected, carefully freed from the muscular tunic, is well washed with water, and then digested with about six ounces of distilled water at a temperature of from 90° to 100° F. After standing for a few hours, the liquid is to be skimmed and poured off clear; the piece of mucous membrane, which is not to be cut into morsels but kept whole, is then washed again, and again macerated with six ounces of cold water; this fluid is by and by to be poured off and filtered, and the same process is to be repeated until the membrane operated on begins to putrefy. The different liquids obtained put together and filtered, and having had a little acetic or hydrochloric acid added to them, forms the artificial digesting fluid. The active principle contained in this fluid is *pepsin*, a peculiar proximate animal principle of such potency, that when in a state of purity, $\frac{1}{60000}$th part added to weakly acidulous water forms a powerful digestive fluid. Coagulated white of egg, meat, bread, &c. &c., added to the digestive fluid prepared in the manner above indicated, and set in a temperature between 30° and

§ 161. The gastric juice, as secreted by the living stomach, is an extremely compound fluid (§ 148). Do the whole of its constituent elements contribute to the work of digestion, or are there only several of them which are essential and efficient, the others being only accidentally mingled with the fluid? This question is easily answered: A solution of pure pepsin in slightly acidulated water dissolves the food as quickly and completely as the natural gastric juice; all the constituents of this fluid therefore other than the pepsin and the acid—the salts and animal extractive—are not essentially necessary to digestion. A simple solution of pepsin in water, however, has no digesting power; articles of food are not attacked and dissolved by it, but on the contrary pass rapidly into putrefaction. A simple dilute solution of an acid aided by a suitable temperature,

35° C. (90° and 100° F.) will be found after a time softened, dissolved, and converted into chyme. The time necessary to effect the change varies between two and twelve hours; it is of course the shorter as the digestive liquid is stronger, as pains have been bestowed in its preparation, and as the temperature is properly regulated in the course of the experiment. But in order to exhibit the phenomena of digestion, it is not even necessary to be at the trouble of preparing a digestive liquid by itself and especially; it is sufficient to add a few pieces of the dry or recent mucous membrane of a stomach along with the articles of food which it is proposed to make the subject of the experiment to some acidulated water, and leave the whole to macerate for a few hours. The experiment of artificial digestion always succeeds if the following particulars be attended to: the temperature both in preparing the digestive fluid and during the experiment should be between 30° and 35° C.; (90° and 100° F.) a lower grade retards the process, a higher one destroys the peculiar power of the fluid entirely. The second point has reference to the quantity of the acid: if to a watery solution of pepsin a small quantity of acid be added, a precipitate ensues (a microlytic precipitate), which is redissolved by a larger quantity of acid. This is the best proportion in which the acid can be used. For if a little more acid be added, a precipitate happens a second time (a microlytic precipitate) which like the microlytic precipitate will dissolve, indeed, in a sufficient quantity of water, but will be found to have lost its solvent properties. The quantity of acid employed ought not, therefore, to be too large. The kind of acid appears to be indifferent; hydrochloric is that which is usually employed, the artificial digestive liquid which it forms appearing to resemble the human gastric juice most closely. If we desire to examine the products of the artificial digestion chemically, sulphuric acid, as the most readily separable, is the most eligible. The quantity of water seems to be of no great moment, for an extremely dilute solution of pepsin still exhibits digesting powers; the quantity of the acid must, however, bear a certain proportion to that of the water.

on the contrary, has the power of dissolving a variety of substances; and several physiologists have consequently thought proper to ascribe the solution by the gastric juice either of articles of food generally, or of some of these, to the free acid which this fluid holds in its constitution. But the solution of various articles of food effected by dilute acids alone is never so complete as that which is performed by the gastric juice, it also requires a longer time, and in addition peculiar favouring circumstances, especially a higher temperature, for its accomplishment. It is therefore imperative on us to conclude that it is the combination of the pepsin with the free acid which accomplishes digestion, and that to the normal act as it takes place in the healthy stomach both substances are required[316].

[316] Tiedemann and Gmelin held that the free acid was the principal agent in effecting the solution; and according to Schwann, many principal articles of food, such as casein, animal jelly, starch and gluten, are dissolved by it. Wasmann, too, maintains that the acid alone possesses the solvent digestive faculty, and that the pepsin only accelerates the process. I had myself, in the course of an earlier series of experiments, been brought to conelude that as acids greatly diluted, in favourable circumstances, especially with the assistance of a temperature between 70° and 100° C. (158° and 212° F.) and a long time, had the power of dissolving almost every kind of food, they were the virtual digestive principle. But when we make two comparative series of experiments, the one with an acidulated solution of pepsin, the other with simple acidulated water, we find that in the former, the temperature being maintained at that of the human body, the solution of the food takes place in the same time and just as completely as it does in the living stomach, which is very far from being the case in the latter. This is enough to force conviction on the mind that pepsin as well as acid is essential to digestion, as it goes on under ordinary circumstances within the stomach. [One cause of the tardy digestion that accompanies the preternatural formation of acid in the stomach, may depend on the precipitation of the pepsin as fast as it is elaborated; but an excess of acid, though the cause of much suffering to the patient, is connected with the least important of all the forms of dyspepsia; there is very perfect solution of the food in the end, and the individual is sufficiently nourished—often even fat and florid, in spite of the misery he endures after every meal. It is in these cases that animal food agrees so well. There is no extra quantity of acid formed from beef or mutton; the patient digests like other people, and feels himself at ease. But the case is very different where the stomach is simply atonic, or where it is in a state of erethism, and therefore inclined to perform its function amiss. Here a hearty meal of animal food—beef or mutton—is either felt as a load which cannot be got rid of, or as the cause of a state of febrile excitement of the most distressing kind. Here the lightest articles of vegetable food and animal broths only, are indicated, as they alone

What then is the theory of digestion? in other words, how do we explain the solution and alteration of the food during digestion upon chemical grounds? The explanations hitherto offered are referrible to three heads: 1st, Digestion takes place in virtue of *catalysis*, that is, pepsin and acid by their mere presence effect the change and solution of the food in the digestive fluid, without themselves combining with it, or suffering any change; 2nd, The digestive principles—the pepsin and associated acid—unite chemically with the constituents of the food, by which this is chemically changed and rendered soluble in the digestive fluid; 3rd, The pepsin suffers change itself, and effects the chemical combination of the acid with the food, and the solution of the latter in the gastric juice. But none of these different views can with certainty be indicated as that which is absolutely the right one[317].

Changes undergone by the food in the Intestines.

§ 162. From the stomach the food in a great measure, or wholly dissolved and changed into chyme, passes into the duodenum, where it is mixed with the pancreatic fluid and the bile. What effect chemically or otherwise the pancreatic juice may have upon the

are readily digested. The worst of all the forms of dyspepsia is that in which the amylaceous principle in all its shapes is changed in the stomach not into lactic or acetic acid but into sugar, a form which I have of late years spoken of in my lectures under the name of the *Dyspepsia saccharigena*, and which is universally known by the title of the Diabetes mellitus. I have in two different instances ascertained that an artificial digesting fluid prepared from the mucous membrane of the stomach of individuals who had fallen victims to Diabetes mellitus possessed as perfect a solvent power over hard white of egg, meat, &c., as another prepared from a pig's stomach. I failed, however, to procure any sugar by the action of this artificial fluid on starch and even on dextrine. R.W.]

[317] The first of these three views is rendered improbable by the circumstance that the pepsin very certainly suffers a change during digestion. Pappenheim has shown that it is no longer precipitated by the nitrate of the protoxyde of mercury after digestion, as it is before this process, the test being one of extreme delicacy. And then, is the admission of a pure catalytic force admissible in chemistry? To me it seems not. It were better at all times to own that this or that phenomenon was inexplicable at the present moment, than to call in the aid of an unknown power as a means of explanation. Forced to choose among the three views, we should say that the third wore the greatest show of likelihood upon its face.

chyme is wholly unknown[318]. We even know very little more of the effects of the bile; it seems to act as a stimulant upon the alimentary canal, exciting its peristaltic motions. The free acid of the chyme must cause decomposition of the bile; some of its constituent ingredients, the choleic acid (bilin and resin of the bile) and the mucus are precipitated. The soda of the bile, on the other hand, combines with the free acid of the chyme, and partly neutralizes it. No other chemical effect of the bile upon the chyme has been accurately noted[319].

318 To say that the pancreatic fluid assists the assimilation of the food must remain without scientific value, so long as we are not informed of the wherein this assimilation consists. [It strikes me that the office of the pancreas is simply to dilute the thick pultaceous mass that passes from the stomach, and so render it more fit to yield its nutritious parts to the action of the absorbents. The stomach is a mere sieve in reference to diluents of all kinds; a pint or more of watery fluid is removed in the course of a few minutes from the stomach, plainly that its presence might not interfere with the due solution of the food; but this accomplished, considerable dilution becomes necessary, and this is effected by the afflux of the pancreatic fluid. R. W.]

319 When bile is mixed with acid chyme a deposit ensues; it has a green colour, and consists of mucus and the substance called choleic acid by Demarcay. The same precipitate falls when instead of acid chyme a diluted acid—muriatic, sulphuric, nitric—is added to bile. Acetic acid occasions no precipitate of choleic acid. Nothing is thrown down from the chyme unless a considerable excess of bile be added to it; it is only after complete neutralization of the chyme that a small quantity of the matter held dissolved in it is precipitated; but Tiedemann and Gmelin always found the chyme of animals to be acid even after the bile had been mixed with it. The old notion that the chyle was precipitated from the chyme in white flocks is, therefore, incorrect; the white flocks are mere mucus, as the distinguished experimenters just quoted showed (loc. cit. B. i. S. 363). My own opinion is, that the bile plays no very important part in digestion; its principal office seems to me to be that of neutralizing a portion of the acid, according to the views of the physiologists of the last age. [With this view I cannot agree. I feel assured that the office of the bile in neutralizing the acid of the chyme is altogether insignificant; this, in fact, is the old struggle between acid and alkali, and I cannot see that there was any necessity for a counterbalancing means of the kind in question. In the first plan, the acid formed during digestion is of a kind which, in contact with vegetable and animal matters, suffers spontaneous decomposition and becomes carbonic acid gas; and when the stomach forms acid in excess, as it often does, were the quantity of soda in the bile multiplied an hundred-fold and more, it would not suffice to neutralize it. R.W.] The principal ingredient of the bile is the choleic acid in combination with soda; its other principles—fat and extractive matter, cannot be supposed to

§ 163. We are very indifferently acquainted with all that happens to the chyme in its passage through the rest of the intestines. A portion of the chyme,—the portion which is in a state of solution, to wit,—is taken up, principally, as it appears, by the intestinal villi, and makes its way into the lacteals, where it forms the chyle. Any part of the food that had escaped complete solution in the stomach, would seem to be dissolved in the intestines[320]. The juices secreted

stand for much in the act of digestion; the cholcic acid, however, is in great measure precipitated and forms part of the feces. I have repeatedly examined the fluid excrements of patients, who for a long time had taken no solid nourishment. The solid constituents of these feces always presented the same appearance under the microscope: an indefinitely granular mass, which resembled in every respect the precipitate obtained from bile to which a diluted acid had been added; the chemical examination confirmed the fact of this identity. If now we conclude, as from my observations as well as those of Tiedemann and Gmelin, we must, that the chief ingredient of the bile is precipitated on its admixture with the chyme, and becomes a portion of the excrementitious matter which is destined to be discharged, the participation of the bile in the process of digestion cannot be much. It has been sought to determine the influence of the bile on digestion, by tying the ductus choledochus communis in animals; Brodie, Tiedemann and Gmelin, Leuret and Lassaigne, all instituted experiments of this kind. The general conclusion come to was, that jaundice was induced, and that the ventricular digestion was not impeded. The experiments of Tiedemann and Gmelin on dogs even showed that the formation of chyle was not interrupted; the chyle in the absorbents of the small intestines, however, was transparent, whereas in the normal state it is white. [This appears to me to be the most important fact elicited by the experimenters in connexion with the function of the bile. The chyle being transparent and watery-looking without the access of bile, white and opaque with its access, it is impossible to overlook some powerful influence which it exerts, although the nature of this has hitherto escaped us. R. W.] According to Purkinje's experiments, the addition of bile disturbed the artificial chymification; biliary resin alone, according to Pappenheim, has the same effect. This explains in part why painful mental emotions and other pathological conditions, which have the effect of causing bile to flow into the stomach should so materially affect digestion. Leuret and Lassaigne held that the bile dissolved fatty substances, and thereby assisted in their digestion; but Tiedemann and Gmelin combated this statement, they having found that bile had no power whatever of dissolving fat. There is no necessity in fact for having recourse to any such virtue in the bile; in the course of our experiments on artificial digestion, we see that the greater part of the fat which is taken as food must be dissolved by the heat of the stomach, and made into an emulsion by its contractions.

320 Tiedemann and Gmelin on many occasions detected unaltered alimentary

by the glands of the intestines probably contribute to this solution[321]. They must also aid, along with the mucus which is poured out by the intestinal parietes, in keeping these lubricated, and so facilitating the transit of the insoluble remainders of the food; more than this, they must prove of essential service in keeping the soluble parts of the chyme in a state of fluidity, and so securing their extraction in their passage through the intestines. The secretion of these juices is excited and increased by the stimulus of the chyme.

§ 164. The chyme of the intestines consists, as already mentioned, of two parts, one which is destined to be absorbed, another which will be voided in the shape of excrement. It were necessary to a complete understanding of the process of digestion to know whether that portion of the chyme which is absorbed, is taken up as it comes from the stomach, or whether it undergoes any farther change. This question cannot for want of positive experiments on the subject be answered definitively at present. We must therefore limit ourselves here to the indication of the changes which the chyme, and particularly that portion of it which is to form the feces, undergoes. For our knowledge of these changes we are principally indebted to the admirable researches of Tiedemann and Gmelin. The chyme of the small intestines consists in general of the same ingredients as that of the stomach, but in smaller quantity; it shows acid reaction, but of a weaker kind than it does in the stomach, even after admixture with the bile; towards the end of the small intestines the acid reaction is still more feeble, and sometimes it has ceased entirely. Here the mass has also become more consistent;

matters in the upper part of the intestine: in the duodenum, for instance, they discovered starch, by the usual test of iodine; towards the end of the small intestine, however, all trace of undecompounded food had disappeared. [If the reports of others are to be trusted, the undecomposed proximate principles of food have been found even beyond the boundary of the intestines. Brande, as has been stated, tells us that he found sugar of milk in the lacteals, and Gerber (*General Anatomy*) says, that he proved the presence of starch in the same vessels by the usual iodine test. These statements, if confirmed, would be extremely interesting; in connection with physiological and with pathological considerations, it would also be very important to show them true or false. R. W.]

[321] There is, however, no occasion to insist on this completion of the process of chymification in the intestines, by the influence of the intestinal juices; it may take place in consequence of the continued action of the gastric juice mingled with the alimentary mass in the stomach.

it seems to consist almost entirely of the parts that are to form the feces, viz: the insoluble particles of the food, the woody fibres, the horny tissues, &c. and of the excrementitious matters which are added to it within the body itself—certain constituents of the bile, inspissated mucus, &c. It would appear, however, that even in the great intestines certain soluble portions were extracted and absorbed from the now excrementitious mass. Some writers will even have it that a kind of second digestion commences in the cœcum in many animals, effected by an acid fluid like that of the stomach secreted by this part of the intestine[322]. Whether any cœcal digestion of this description takes place in man or not is unknown; but this much is certain, that if it does happen, it is of no such great importance as the process which occurs in the cœcum of many animals, the horse for example. It is in the great intestines that the formation of feces begins; in other words, the portion of the alimentary mass which is insoluble, and not susceptible of being absorbed, and which must therefore be rejected, becomes of a darker colour and acquires a peculiar fetid smell. Whether the change that here occurs be the effect of a peculiar secretion of the great intestine or of spontaneous decomposition—a kind of putrefaction of the remainder of the food itself,—has not been determined[323]. The chemical constituents of human feces are not always the same; water, mucus, a variety of salts, and the principal ingredients of the bile can always

[322] In the horse, to wit, and the majority of the rodents. In the horse, however, the secretion of the cœcum contains no free acid.

[323] Chevreul and Majendie examined the gases in the intestines of several executed criminals. Numbers 1 and 2, two hours before their death, had partaken of bread and cheese, and drunk some wine and water. Number 3, four hours before execution, had eaten bread, meat, and haricots, and drunk some red wine. The gases of the small intestine in 100 parts consisted, in number 1, of 24,39 carbonic acid, 55,53 hydrogen, 20,08 azote. In the great intestines they consisted of 43,50 of carbonic acid, carburetted hydrogen with traces of sulphuretted hydrogen, 5,47, azote, 51,03. In number 2, in the small intestine, 40,00 carbonic acid, 51,15 hydrogen, 8,85 azote; in the great intestine, 70,00 carbonic acid, carbonic acid and carburetted hydrogen 11,60, azote 18,40. In number 3 in the small intestine 25,00 carbonic acid, 18,40 hydrogen, 66,60 azote; in the cœcum 12,50 carbonic acid, 7,50 hydrogen, 12,50 carburetted hydrogen, 67,50 azote; in the rectum 42,86 carbonic acid, 11,18 carburetted hydrogen, 45,96 azote and a small quantity of sulphuretted hydrogen. It is obvious, therefore, that the gases, though very uniformly the same, vary greatly in their relative proportions.

be detected in them ; the other parts vary with the nature of the food[324].

CHAPTER IV.

OF RESPIRATION.

Of Respiration in General.

§ 165. In the higher animals the whole of the circulating fluid is sent through a special organ formed on the same general plan as the secreting glands, which fulfils incessantly an office the most essential to life ; this organ is the lung, or speaking in the plural, the lungs. In the lungs the mass of the circulating fluid, which had been changed in the periphery of the body into venous blood, mixed with the lymph collected from all parts and the newly elaborated chyle taken up from the intestines, is brought into intimate contact with the air of the atmosphere, the effect of which is that the blood recovers its bright colour, or acquires the arterial character, which is alone competent to minister to nutrition, and properly to stimulate the central parts of the nervous system and the apparatus of motion, and which also, with the single exception of the liver, furnishes their materials to the various organs of secretion.

Form and intimate Structure of the Respiratory Organs.

§ 166. Few organs present such varieties in point of structure in the animal series as the apparatus of respiration. In the lowest classes of all it even seems to be entirely wanting—in the entozoa, polypes, medusæ, and many other creatures besides, we have no traces of a particular respiratory system. Here nevertheless there is a substitute for the special organ in the general surface of the soft and delicate body, which is of course in contact with the air that is held dissolved in the medium surrounded by which they live,

[324] Berzelius made a quantitative analysis of human feces. 100 parts contained 75,3 water, 24,7 solid matter, which last consisted of bile, albumen, and extractive matter, and of salts soluble in water 5,7, insoluble remains of the food 7,0. In the small intestine, on the contrary, the solid matters were mucus, biliary resin, fat, animal matters, &c. 14,0.

or otherwise the water is taken into the stomach and intestinal canal, or it is drawn into the interior of the body and made to penetrate between and to bathe the whole of the viscera. In this way it is brought into contact with the vessels, through the delicate walls of which that peculiar influence is readily exerted which goes on among the higher classes of animals through the membranous tissues of the lungs in immediate contact with the air of the atmosphere. In many of the less perfectly organized inhabitants of the ocean, star-fishes, sea-urchins, &c., we find the whole interior of the body full of sea water, and observe particular organs to secure its perpetual renovation[325].

§ 167. The greater number of animals, even of the invertebrate series, possess particular organs of respiration. In some cases however, where these exist, we still find a provision for the assumption of water charged with air, as a kind of complement to the proper respiratory system. In the foot of many of the univalve and bivalve molluscs, for instance, the organization of which is sufficiently complex, we observe particular openings which lead to canals that pass through the foot and conduct water into the cavities of the body.

§ 168. The respiratory apparatus of other animals can be arranged into three principal forms: 1. Lungs; 2. Gills; 3. Tracheæ. In the two first of these forms of the respiratory organ, the tendency of glandular organs in general is apparent, the tendency, namely, within the smallest possible space to compress the greatest extent of membranous surface, upon which blood vessels in great numbers are distributed and brought into contact with an external medium. This tendency, indeed, both as regards gills and lungs, is accomplished in the most complete manner imaginable, the whole circulating fluid of the body, in the vast majority of animals, being here spread out upon membranous structures of comparatively small magnitude, and so brought into mediate or immediate contact with the air of the atmosphere.

§ 169. When the membranous surface which is to serve as the means of contact between the circulating fluid and the air is invert-

[325] The view given here of the principal forms of the organs of respiration in the animal series is very general; for particular details I refer to my *Comparative Anatomy* and *Icones Zootomicæ*.

ed and contained within the interior of the body, so as to form a simple sac, or a more complex aggregation of cœcal sacs and vesicles, the organ is designated a *lung*. If, on the contrary, the membranous surface is everted and extended in the form of laminæ, tufts, ramified lappets, &c. which may be contained in a cleft of the body, or attached to some particular part, or distributed over the whole of its external surface, the organ is known by the name of *gills*. As a general rule, lungs are only met with in animals that live on the land, or in those that though they live in water, must still spend some portion more or less of their time on the surface for the sake of air ; and gills, on the contrary, are only met with in purely water-animals, which however do not breathe water, but the air which it always holds dissolved[326]. Still these are not universal rules ; for there are animals which take the water in which they live into internal cavities and canals, even hollow ramified sacs, formed in all essential respects on the type of the lungs of air-breathing animals[327] ; and there are air-breathing land animals upon the pulmonic sacs of which leaf-like gills are attached[328].

§ 170. The third form of respiratory apparatus or *trachea* is general among insects, and also occurs in many arachnidans. The tracheæ are air-tubes which divide and become finer and finer, here and there enlarging into vesicles of different sizes, and so penetrating every organ of the body. They convey the air of the atmosphere to the interiors of all the tissues, and as they are everywhere surrounded by the blood, which we have seen to be shed at large into the interstices of the body, and not to be contained within any thing like determinate canals or blood vessels (§ 111), the contact and mu-

[326] The experiments of Humboldt and Provençal have shown that the water of every kind in which living creatures live, contains oxygen and azote in determinate proportions dissolved in it; the gases are absorbed from the atmosphere and expelled by boiling; fishes soon die in water that has been freed of its air in this way; they also die when they are kept at the bottom of vessels of limited capacity, and not suffered to come to the surface to breathe the upper strata of water, which, being in contact with the atmosphere, are never exhausted of their vital fluid.

[327] To this category belong Ascidiæ, for example, (*Icones Zootom.* Tab. xxxi.) which suck the surrounding water into hollow sacs, upon which leaf-like offsets are observed; and Holothuriæ, (*Icones Zootom.* Tab. xxxii.) in which a hollow tubulus arises from the cloaca, which ramifies like the branches of a tree, and expands into hollow terminal vesicles.

[328] The pulmonic Arachnidans, for example. (*Icones Zootom.* Tab. xxv.)

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tual interchange of elements between the two fluids is readily accomplished.

§ 171. The different forms of the respiratory organ present themselves in the most varied arrangements and combinations of its essential elements. There are entire orders of animals, frogs and newts, for example, the larvæ of which breathe by gills and the fully formed animal by lungs; or lungs and gills occur together through the whole course of existence, as in the proteus and its congeners, and in many molluscs[329]. In many spiders we find gills, lungs and tracheæ; or otherwise, and this is observed in the larva of the ephemera, the tracheæ divide upon external gill-like laminæ. Gills present the greatest imaginable variety of form in the different classes and orders of animals in which they occur, from the state of simple filaments and plates, to the most complex pectiniform, branched, and feathered or plume-like structures.

§ 172. The minute anatomy of the lungs in vertebrate animals exhibits many interesting varieties. The structure is simplest in the naked amphibia, where it is but little more complex than in the snails[330]. In the water-newt, for instance, the lungs present themselves as a pair of simple elongated sacs (Fig. CLXXIV.) attached to an extremely short rudimentary larynx, and internally exhibiting no projection; the air distends the entire hollow internal sac or cavity. In the frogs the membranous surface of the lungs is increased by the development of cells upon their internal aspect, (Fig. CLXXVI.), upon the bottoms of which cells, other secondary and smaller ones can be perceived. All these pulmonic cells, however, are merely parietal, and communicate directly with the middle cavity of the lung, which is filled with atmospheric air, and upon the membranous walls of which, as well as upon their bottoms, the blood vessels ramify. In the turtles and crocodiles the cellular subdivisions increase in number and decline in size, and the common cavity is divided by various bands and septa stretching across it into a number of mutually communicating sacs or pouches. The whole lung thus acquires a more compact or parenchymatous appearance. In the serpents, in which one only of the two lungs is

329 For example, in the genus Onchidium.

330 The lung presents itself in its very simplest form in the snails and slugs. The contractile respiratory orifice here leads to a simple smooth internal cavity lined with a delicate mucous membrane, upon which the pulmonary vessels are distributed.

ever completely evolved, this at the upper part is covered with small parietal cells; but these gradually become smaller and smaller, less and less distinct, and finally disappear entirely, so that the lower part of the lung is completely vesicular and unvascular.

§ 173. In the class of birds we observe in the same interesting manner the general type of the lung preserved, but the surface of contact greatly increased by means of parietal cells, which are repeated again and again. This modification is made necessary by the larger quantity of blood which is here transmitted to the respiratory system, and the consequent augmented amount of respiratory process, by which a larger extent of membranous surface became indispensable. The bronchi in birds are continued into the lungs, where they divide into membranous tubes, which permeate their substance. The deeper tubes stand like organ-pipes, and open into the superficial tubes; and all are covered with small parietal cells upon which vessels are distributed. The cells form very elegant, delicate microscopic reticulations, and generally present themselves as six-sided spaces.

§ 174. The lungs of man and the mammalia are formed after another and a different type. The trachea here divides and subdivides like the branches of a tree, into finer and finer branches, which at first contain cartilages in their constitution, but which by and by

Fig. CLXXIV.

Fig. CLXXIV. Lung of the Water-newt (Triton cristatus): A. the natural size; B, magnified: *a*, Pulmonary artery; *b*, Pulmonary vein.

become membranous, and finally end in blind sacculi, or rather in hollow berry or bud-like and clustered vesicles (Figs. CLXXIX. and CLXXX). The pulmonic cells of man and the mammalia, consequently, are not parietal but terminal cells; they vary from the 6th to the 18th of a line in magnitude, the majority of them measuring between the 8th and the 10th of a line in diameter. Delicate arcuate fibres, of the nature of elastic tissue, surround these terminal vesicles, and hold them distended[331], whilst the vessels spread freely over their surface (Fig. CLXXXI).

[[331] Surely this is not the case; we generally ascribe the *collapse* of the lungs which takes place when the cavity of the chest is laid open, to the action of the elastic element in their composition. The air-cells are distended in man and mammals by the dilating force of the thoracic grating, acted on by its appropriate muscles, and the diaphragm. Mr. Gulliver informs me that an examination of the lungs of man and the lower mammalia has even led him to infer that the elastic tissue is an important agent in expiration. This tissue, he says, may be seen to invest the entire surface of the lung, forming a strong, elastic, though delicate capsule to the organ. If the pulmonary pleura of the horse be stripped off, for example, and the surface of the lung be then examined, it will be found to be invested by a mesh of fibres, resembling those of the ligamentum nuchæ of this animal, and of the fibrous coat of the aorta of the ox, as depicted in Gerber's *Anatomy*, figs 54 and 55. I may add, that Mr. Gulliver, availing himself of the characteristic microscopic appearance of the tissue surrounding the air-cells, has been enabled to detect tubercular matter filling *the cavities of these cells*, by examining either very thin slices and fragments, or softened portions of deposits, which to the naked eye appeared to be only homogeneous masses of tubercle. A figure from one of Mr. Gulliver's observations is here given, because the actual seat of tubercle of the lungs has long been an interesting question to physiologists as well as to pathologists. R. W.]

Fig. CLXXV.

Fig. CLXXV. To the left, magnified 190 diameters, is shown a central portion of tubercle from the lungs of a man aged 22 who died of pulmonary consumption; the tubercle is contained in the air-cells, and surrounded by the fibres of their walls. To the right is depicted some of the same tubercle separated and magnified about 820 diameters.

§ 175. The development of the lungs is extremely interesting. In the embryo of the bird and mammal they first appear in the shape of a simple and then of a double projection from the œsophagus (Fig. CLXXXII. *a*), which soon divides more distinctly into two, becomes separated from this part, and is finally supported upon

Fig. CLXXVI.

Fig. CLXXVI. Portion of the lung of the Triton cristatus. The vessels are injected with fine size and vermilion, and form so dense a net that minute islets only of parenchyma remain visible.

Fig. CLXXVII.

Fig. CLXXVII. Portion of the Frog's lung from within, to show the open parietal cells—figure drawn twice the size of nature.

Fig. CLXXVIII.

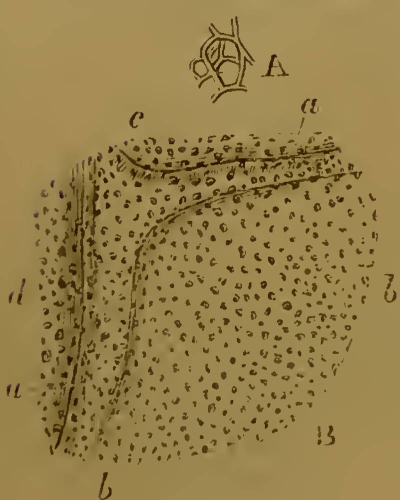


Fig. CLXXVIII. A. Several cells from the lung of a Tortoise. A portion of one of these cells is exhibited in B magnified 500 times—part of the septum, *a a*, which divides this cell from those next to it, *c* and *d*, is seen. The vessels are injected with size and vermilion, and form such thick masses that the islets of pulmonic parenchyma betwixt them almost disappear.

a pedicle—the future trachea (Fig. CLXXXII. *b*). In birds these little sacs are then drawn out into hollow tubes, which pass over into the parallel pipes above described (§ 173.) In mammalia they divide after the manner of branches into twigs and minute vesicles (Fig. CLXXIX), which advance in development and become the future terminal cells[332].

[332] In studying the development of the pulmonic system, the young embryos of the fowl, hog, and sheep, are the best subjects. The structures are very readily

Fig. CLXXIX.

Fig. CLXXIX. A piece from that part of the Serpent's lung which is most scantily supplied with vessels, magnified 400 times. The vessels here form a very beautiful rete with wide meshes; they have been successfully injected with fine size and vermilion.

Fig. CLXXX.

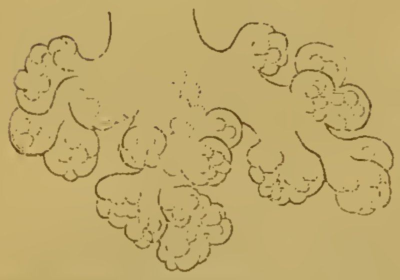


Fig. CLXXX. Terminal vesicles of the human lung, hanging to a branch of the bronchi as berries hang to their stalk, and distinct from one another. The figure is half a plan, and the magnifying power used very high.

Fig. CLXXXI.

Fig. CLXXXI. A. Portion of the lung of a Hog. The terminal vesicles are filled with mercury, and of the natural size. B, the same part seen under a simple lens.

§ 176. The capillary vascular net-work of the lungs, as already stated § 123, exhibits a peculiar structure, which may be studied very readily

followed in their different phases. On the structure of the lung vide Reisseisen, *De fabrica Pulmonum*, fol. 1822. On the development of the respiratory apparatus of birds see Rathke in *Acta Acad. Cæsar. Leopold. Naturæ curiosorum*, vol. xiv. pars. 1.

Fig. CLXXXII.

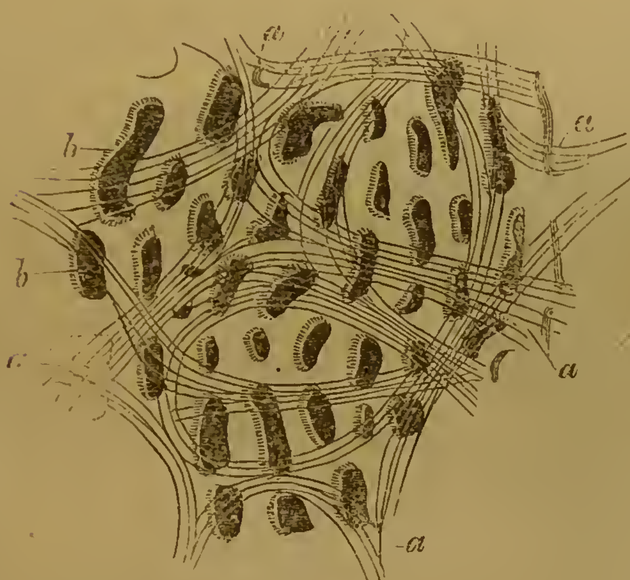


Fig. CLXXXII. Small portion of lung from the body of a man examined shortly after death, under a magnifying power of 200 times. The vessels, *b b*, &c., still turgid with blood, include very minute islets of parenchyma between them; the semicircular fibres *a a a*, surround the smallest terminal cells of the lungs.

Fig. CLXXXIII.

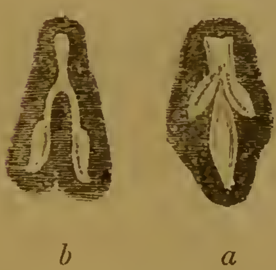


Fig. CLXXXIII. *a*, Rudiment of the lung in the embryo of the Fowl of the fourth day; *b*, The lung in the embryo of the sixth day. Both figures twice the size of nature.

Fig. CLXXXIV.

Fig. CLXXXIV. The greater part of the right lung of a fœtal sheep, $1\frac{1}{4}$ inch long, seen under the microscope, (after Müller, *De Gland. secern. struct. penit.* T. xvii. f. 7.)

in the lungs of the live newt (Figs. CLXXXV. and CLXXXVI.) or in preparations of the same part that have been finely injected.

Fig. CLXXXV.

Fig. CLXXXV. Termination of one of the branchings of the bronchi from the lung of a very young embryo of the hog after Rathke (Fig. viii. T. xviii.)

Fig. CLXXXVI. (Repetition of Fig. CLXV.)

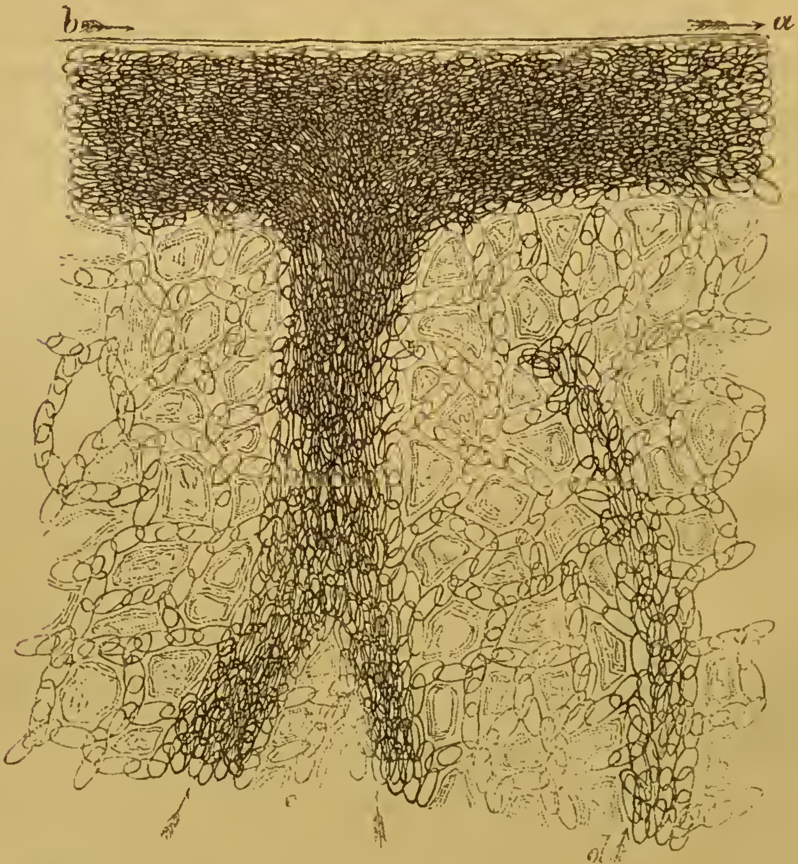


Fig. CLXXXVI. Portion of the lung of a live newt, magnified 150 diameters. On the upper margin of the figure, the great stream of venous blood is observed proceeding from *b* to *a*, this principal stream being joined by another, *c*, made up of two lesser currents, anastomosing with which, numerous capillaries are seen proceeding from or in direct communication with a branch of the pulmonary artery, *d*. The very delicate capillaries which serve as bonds of union between the two kinds of pulmonary vessels, are observed playing around little islets of the substance of the lung, in which a granular or cellular texture is indistinctly perceptible. The clear space between the current of the blood and the solid and always obvious walls of the vessels constantly seen in the larger branches, is almost entirely wanting here. The lymph-granules, therefore, are observed mixed with the general torrent.

From the whole extent of the pulmonary artery a vast number of very small arteries arise, the orifices of which give the inner surface of its principal branches the appearance of a regularly perforated sieve; these minute vessels form a very close irregular hexagonal intermediate net-work, without resolving themselves into branches and twigs like a tree, and so forming a capillary rete. Yet single larger vessels (Fig. CLXXXV. *d*,) do proceed from the pulmonary artery to reach some more remote part of the lung. The pulmonary vein, like the pulmonary artery, is partly perforated at every point in its course for the reception of smaller vessels, and is partly formed by larger venous trunks, which collect and bring the blood from greater distances. (Fig. CLXXXV. *c*). The islets of the thin and indistinctly cellular parenchyma are often of a diameter inferior to that of the vessels which surround them; this is the case in the tortoise, for example (Fig. CLXXVII.), and appears to be the case in man also (Fig. CLXXXI). It is remarkable that even in the more conspicuous branches of the pulmonary vascular system, the layer of transparent lymph in immediate contact with the walls of the vessels should either be wanting or of the greatest delicacy; and that no lymph-corpuscles should be visible swimming in it apart from the general current, but that they should be observed mingled with the common stream. (Fig. CLXXXVI. *a*, *b*, *c*)[333].

[333] On the respiratory movements, the influence of the nerves on respiration, &c. see the paragraphs devoted to the consideration of these subjects in the chapter on Motion in General. There are good representations of the capillary net-work of the lungs in the newt, the toad, &c. in Dr. M. Hall's *Critical and Experimental Essay on the Circulation.*

Fig. CLXXXVI. (Repetition of Fig. CLXVI.)

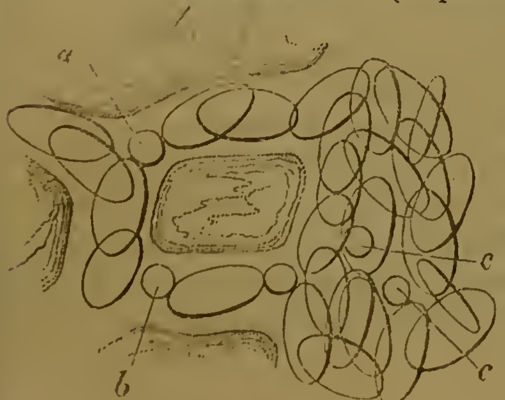


Fig. CLXXXVI. One of the pulmonary islets of the newt bounded by capillaries on three sides, by a larger venous branch on the fourth side. *a*, *b*, *c*, are lymph-globules mingled with the blood-globules. The object is magnified about 300 times.

CHEMICAL PROCESSES OCCURRING DURING RESPIRATION.

(BY DR. JULIUS VOGEL.)

§ 177. The organs which serve in man and the various orders of animals for respiration, and the mechanical part of the function of these organs, have now been described. The very essence of respiration, however, consists in this: that the air of the atmosphere brought into contact with the blood within the lungs effects certain changes in that fluid which are indispensable to the maintenance of life. The air it is true does not come into direct contact with the blood even in the lungs, but is separated from it by the parietes of the pulmonary cells and the walls of the blood-vessels. The air, however, readily penetrates these moist tissues, for it combines with the watery fluid which permeates them, and so makes its way even immediately to the blood[334]. As the lungs contain air at all times, the influence which the elastic fluid exerts upon the blood and the changes which the blood undergoes are not connected with the alternate assumption and rejection of so much air. These are but means to an end: the proper respiratory process, or that process for which inspiration and expiration are instituted, goes on incessantly. Inspiration and expiration are merely provisions for changing the air, which must be renewed at intervals, longer or shorter, if the object of respiration is to be attained.—Before entering on the peculiar chemical processes that occur in respiration, in other words, before condescending upon a *theory of respiration*, it is proper that we inquire into the changes which, 1st the *air*, and 2nd, the *blood* experience in its course[335].

[334] The penetration of the moist parietes of the air-cells and blood-vessels is a general physical phenomenon, and independent of any peculiar power or property inherent in the lungs; any moist animal membrane without or within the living body is gradually penetrated by the air of the atmosphere and other gases. The extensive subdivision which the blood undergoes in the minute vessels of the lungs is obviously calculated greatly to assist the operation of the air.

[335] Besides the researches, now of older date, of Lavoisier and Seguin, of Sir Humphrey and Dr. John Davy, of Allen and Pepys, and others, which are all highly interesting in connection with the subject of respiration, the inquiries of Müller (*Physiology*, vol. i. p. 330), deserve to be particularly consulted; so also do those of T. W. Bischoff, (*Comm. de novis quibusdam experimentis chemico-phy-*

§ 178. The earliest accurate researches into the nature of respiration were instituted with a view to determine the changes which the air experienced in passing through the lungs, and our information upon this part of the function may be said to be pretty full. The air of the atmosphere consists, as is well known, of a mixture of the azotic and oxygen gases, with a slight addition of carbonic acid and of hydrogen gas: 100 parts of atmospheric air consist, according to the latest analyses, very constantly of 79 parts of azote, and 21 of oxygen; the admixtures of carbonic acid and hydrogen, on the contrary, are extremely variable in amount; the carbonic acid has been ascertained to vary between 0,0003 and 1,0 per cent; the hydrogen may amount to about 1 per cent. The air that is expired yields very nearly the same quantity of azote as the air that is inspired; but it contains less oxygen, and a larger quantity of carbonic acid, and also of hydrogen; it likewise contains some volatile organic matters[336]. The quantities of the oxygen and carbonic acid in the air have altered relatively during respiration in suchwise that the volume of the oxygen which has disappeared is rather greater than that of the carbonic acid which has made its appearance. Sir Humphrey Davy breathed during one minute, making 19 inspirations in the time, 161 cubic inches of air, which in 100 parts consisted of 72,7 azote, 26,3 oxygen and 1,0 carbonic acid; and during this time he expired 152 cubic inches of air, of which 100 parts contained 73,4 azote, 15,1 oxygen and 11,5 carbonic acid. In this experiment, consequently, if we disregard the disappearance

siologicis ad illustrandam doctrinam de Respiratione institutis, Heidelb. 1837;) and of G. Magnus, On the Gases contained in the Blood (in Poggendorff's *Annalen*, Bd. 40, p. 583, et seq. [Dr. Davy's more recent observations, which seem to have been conducted with consummate care and skill, were made since those of Bischoff and Magnus. Dr. Davy's results were published in the *Philosophical Transactions* for 1838, and are now included with some additions in his *Researches, Physiological and Anatomical*, 2 vols. 8vo. 1839. See vol. ii. p. 135, et seq. R. W.]

336 The presence of volatile organic matter in the breath is easily demonstrated, by the following simple experiment: breathe several times into a clean jar or bottle and stop it close. After a while drops of water are deposited on the sides which is limpid and clear at first, but which, kept for some time, grows turbid, begins to putrefy, and evolves an unpleasant smell of sulphuretted hydrogen.

of 9 cubic inches of air and a slight increase of azote, it appears that from the respired air 11,2 per cent of oxygen had vanished and 10,5 per cent. of carbonic acid had appeared. In the experiments of Allen and Pepys 100 parts of expired air were found to consist of 79 azote, 13 oxygen, and 8 carbonic acid; supposing therefore the air which was breathed to have been of the normal constitution, 8 per cent of oxygen had disappeared and rather more than 8 per cent of carbonic acid had been evolved. Like results were come to by Dulong, Despretz, Lavoisier, and Seguin. In the quantity of the absorbed oxygen and of the added carbonic acid, however, the statements of the different observers differ: Davy for example found that the quantity of the added carbonic acid amounted to from 3,95 to 4,5 per cent.; in the particular experiment quoted above it was as much as 10,5 per cent. Allen and Pepys state it at from 8 to 8,5 per cent.; Berthollet at from 5,53 to 13 per cent.; Menzies at 5 per cent.; Prout at from 3,3 to 4,6 per cent.; Murray at from 6,2 to 6,5 per cent.; Fyfe at 8,5 per cent. and Irvine at 10 per cent.* The mean of the whole of these observations is about 5,8 per cent. If we presume that errors had crept into some of these experiments, it is still obvious that the quantity of carbonic acid eliminated by different individuals and at different times is not always the same. Prout, whose skill in observation inclines us to place the most implicit reliance on his results, found by direct experiment that the time when the smallest quantity of carbonic acid was produced was shortly after midnight; it increased towards morning, and rose continually till towards midday, when it attained its maximum; in the afternoon it declined again, and sank continually through the course of the evening until it reached its minimum about midnight. The formation of carbonic acid therefore experiences regular fluctuations in accordance with the times of the day. Prout observed, farther, that a larger quantity of carbonic acid was produced in states of

[* From Dr. Davy's most recent observations, it would seem that the absorption of oxygen by the blood is influenced by the season. He infers that the higher the atmospheric temperature and the less the necessity for the production of animal heat, the less difference is there between venous and arterial blood, and the less power has the former of combining with oxygen, and of forming or evolving carbonic acid gas. See his *Researches, Physiological and Anatomical*, vol. ii. p. 140. R. W.]

mental tranquillity, during gentle exercise and with a low state of the barometer; and that on the contrary, less was formed under the influence of active exertion, depression of mind and the use of spirituous liquors. The estimates which we have of the absolute quantity of carbonic acid eliminated during a given time also vary greatly. According to Lavoisier and Seguin, the quantity formed in 24 hours amounts to 8534 grains French; according to Davy it is 17811 grains English; according to Allen and Pepys it is 18612 grains English. But these quantities Berzelius has shown are far too great with reference to the quantity of food consumed in the same interval of time[337]. The quantity of water contained in the expired air amounts, taking the mean of the estimates of a great number of observers, to about 8000 grains, or one pound in the four-and-twenty hours[338].

[337] Berzelius observes, (*Thierchemie*, 3tte Auf. S. 124,) that upwards of six pounds of solid aliment daily would be required to replace this loss of carbonic acid, even were the whole of the carbon of the food to be eliminated by the lungs in the shape of carbonic acid, and none to pass off with the feces, the bile, the urine, &c.; which, however, is very far from being the case. The above quantities must therefore be looked upon as exaggerated, though the observations themselves may be perfectly correct; the error probably lies in the reckoning; during the short period that such experiments last—one or two minutes—inspiration and expiration are almost certainly forced or exaggerated; the air is more rapidly changed, and more carbonic acid is eliminated than during ordinary respiration. The indications afforded by two minutes, under such circumstances, applied to the whole of the twenty-four hours, obviously raise the general result far above the proper standard.

[338] See Müller's *Physiology* by Baly, vol. i. p. 330. The statements in the text refer particularly to the human being; but they also apply very closely to animals which breathe by lungs, with this difference, that in cold-blooded animals the quantities of oxygen absorbed, and of carbonic acid eliminated, are relatively smaller. Dulong found, no matter what animal he made the experiment upon, that there was rather more oxygen absorbed than carbonic acid evolved. The excess in graminivorous animals amounted to one-tenth, in carnivorous creatures it was from one-fifth to one-half, more than the carbonic acid. Despretz observed the same thing. Allen and Pepys, on the other hand, found the quantity of oxygen that disappeared, and of carbonic acid that was generated, to be equal. [The oxygen which disappears, is used up in the combustion of hydrogen, the product of which is watery vapour. R. W.] Treviranus and Müller instituted comparative experiments upon the respiration of some of the lower animals, and the quantity of carbonic acid formed in a given

Respiration in Gases other than Atmospheric Air.

§ 179. With a view of obtaining still more precise information regarding the changes induced in air by its assumption into the lungs, experiments have been instituted on the respiration of different kinds of gas. These experiments, however, almost necessarily extended to the consideration of the effects which breathing different gases produced upon the organism, as well as to the changes which the gases suffered in the process. We shall therefore here consider the two together. During healthy respiration the atmospheric air that supplies the lungs is constantly changed. If this renewal of the air is not provided for, but the same air is breathed over and over again, the circumstances attending respiration are altered. In the same proportion, for example, as the oxygenous contents of the air diminish and the carbonaceous contents increase, less and less oxygen is absorbed, less and less carbonic acid is evolved; and when the air comes to have a certain proportion of carbonic acid mixed with it, which, from the experiments of Allen and Pepys, appears to be 10 per cent., no more carbonic acid is formed, and the elastic fluid no longer suffices for respiration, although it still contains something like 10 per cent. of oxygen. A little oxygen, indeed, continues to disappear, but the respiration

time, contrasted with the weight of the animal, from which it appears that mammals, for every 100 grains of their weight, produce 0,52 of a cubic inch of carbonic acid in 100 minutes; that birds, considered in the same way, produce 0,97 of a cubic inch; that amphibia, (the frog,) still considered in the same way, produce 0,05 of a cubic inch. The respiratory process performed by the medium of water is precisely the same as that which goes on with the direct contact of air: the air dissolved in the water comes into contact with the blood which circulates through the gills, and oxygen disappears and carbonic acid appears as usual. Water in general contains from 5 to 5¼ per cent of its bulk of air dissolved in it,—this air, however, having a somewhat greater relative proportion of oxygen than the air of the atmosphere, oxygen being somewhat more soluble in water than nitrogen. We have very admirable researches on the respiration of fishes by A. von Humboldt and Provençal. The water in which the fishes were put in these experiments contained 20,3 per cent. of air, which in 100 parts consisted of 29,8 oxygen, 66,2 azote, and 4,0 carbonic acid. After having been used for respiration, the water still contained 17,6 per cent. of air, which consisted in 100 parts of 2,3 oxygen, 63,9 azote, and 33,8 carbonic acid. Here, therefore, oxygen was also absorbed and carbonic acid evolved.

becomes laborious, and cannot be carried on without imminent risk of suffocation to any of the higher animals. This is the source of the oppressive sensation experienced when many persons crowded together in a limited space, continue to breathe the same atmosphere. In pure oxygen gas respiration goes on as readily as in atmospheric air, but a feeling of uneasiness and of exhaustion is soon experienced. The changes produced in the gas are of the same nature as when the common atmospheric air is breathed,—oxygen disappears and carbonic acid is engendered; the quantity of the latter, according to Allen and Pepys, being however greater than under ordinary respiration,—it amounts, instead of 8 per cent., to between 11 and 12 per cent[339]. The same experimenters also found that azotic gas was evolved during the respiration of oxygen gas. Nitrous oxyde gas, (consisting of 64 azote, 36 oxygen,) like oxygen, will support life for a time, but it produces a peculiar intoxicating effect upon the economy. A portion of the gas is dissolved by the blood, which assumes a purple red colour; and the face and hands, in consequence of this change, acquire a livid and cadaverous hue. Azote and traces of carbonic acid are found in the expired nitrous oxyde gas. Pure azote, although it can be taken readily into the lungs, and is not at all poisonous, is quite incompetent to support life; small animals immersed in it therefore soon die asphyxiated. Pure hydrogen, too, can be breathed, but will not support life; it is either without effect on the economy, or exerts a soporific influence. The experiments of many inquirers, however, have shown that cold-blooded animals, such as frogs, can exist for hours in pure azote and hydrogen; they become asphyxiated at length, and are apparently dead, but if not kept too long immersed in the gases, they recover when brought into contact with the air of the atmosphere. All observers, too, are agreed that these animals eliminate carbonic acid when confined in azote and hydrogen[340]. In a mixture of four parts hydrogen and one part (volume)

[339] Lavoisier and Seguin ascertained that the quantity of carbonic acid gas produced during the respiration of oxygen was not greater than that which, under similar circumstances, was evolved by breathing atmospheric air.

[340] Spallanzani, Collard de Martigny, and particularly Müller, Bergemann and Bischoff, were the contrivers of very interesting experiments on this subject. Vide Müller's *Physiology*, and the work of Bischoff already quoted.

oxygen, animals were found by Allen and Pepys to become sleepy, without any prejudicial effect upon the health appearing to ensue. Oxygen disappeared and carbonic acid was evolved precisely as when atmospheric air was breathed; at the same time, however, azote made its appearance, and in such quantity too, that in the course of an hour the volume eliminated, equalled, and even exceeded by a half the volume of the animal which was the subject of experiment. Other gases are true poisons to the economy,—carburetted, phosphuretted, sulphuretted, arseniuretted hydrogen, &c. Air that contained no more than $\frac{1}{1500}$th of its bulk of sulphuretted hydrogen was sufficient to prove fatal to a bird: $\frac{1}{800}$th destroyed a dog, $\frac{1}{250}$th killed a horse. Some gases inspired in a state of purity, or but little diluted, induce spasm and complete closure of the glottis, and consequent death; more largely diluted, they excite violent cough. To this list belong chlorine, the vapour of iodine, nitric oxyde, ammoniacal gas, fluoboric and fluosilicious gas, and the greater number of the strong acid vapours, such as those of nitric acid, sulphuric and sulphurous acid, succinic acid, &c. &c.

The greater number of the particulars related in the preceding paragraph have been made known to us through the admirable researches of Sir Humphrey Davy.

CHANGES PRODUCED IN THE BLOOD BY RESPIRATION.

Distinction between Venous and Arterial Blood.

§ 180. The changes which the blood undergoes by respiration cannot be immediately observed; we have hitherto been obliged to examine the blood as it was proceeding to the lungs and as it was coming from them; and have then concluded that any manifest difference between the two is the effect of the exposure it has undergone in these organs. The differences between venous and arterial blood are these: venous blood is of a deep or black-red colour; arterial blood, on the contrary, is of a bright or florid red. This alteration of colour in the blood takes place visibly in the lung, and in consequence of the action of the atmospheric air. Even out of the body venous blood exposed to the air assumes a bright red colour[341].

[341] The change from the deep dusky to the bright red, bears reference, we

The dark coloured blood, as contained in the pulmonary artery, in relation to its solid constituents, is somewhat more watery than aortic arterial blood; the blood consequently loses a little water in the lungs[342]. Albumen, extractive matters, salts and fat, exist in both kinds of blood in like quantity. Arterial blood contains more fibrine than venous blood; it also coagulates more quickly, and forms a firmer and more

naturally conclude, to the colouring matter of the blood,—the hæmatin. But whether this principle suffers any chemical change or not, is unknown. Michaelis subjected the colouring matter of arterial and of venous blood to a comparative elementary analysis, and found that the arterial contained more oxygen and less carbon than the venous. But this analysis, however probable its results, must when critically examined be held as inconclusive. It is impossible, for example, at the present time, to separate the colouring matter of the blood from its other principles and be quite certain that it had suffered no change in the process of separation;—it were not too much to maintain that the alterations impressed by the most careful chemical analysis must be much greater than those which take place in the delicate process of respiration. The brighter colour of arterial blood has been supposed to be connected with the evolution of carbonic acid, which is well known to occur in the course of the respiration (see the following paragraphs); but this view is not tenable; for arterial blood itself contains carbonic acid, and venous blood, which has been shaken up with hydrogen gas, and thus freed from the greater part of its carbonic acid, still remains deep-coloured,—it becomes a little brighter, indeed, but not nearly so bright as arterial blood. As venous blood only acquires the florid red of arterial blood in those gases or mixtures of gases which contain oxygen, it is probable that the change of colour which occurs in respiration is connected with the absorption of oxygen as well as the elimination of carbonic acid. It must not be forgotten, however, that many of the neutral salts,—common salt, nitre, sal ammoniac, &c., added to the deepest coloured venous blood, give it in an instant the bright hue of arterial blood. [Dr. Davy observed that venous blood does not acquire the arterial hue when deprived of carbonic acid by the air-pump, and that the same blood becomes scarlet from the absorption of oxygen without the disengagement of any carbonic acid; he also found that venous blood assumed the scarlet colour when agitated with a mixture of carbonic acid and oxygen gas, and when it absorbed a relatively much larger quantity of the former than of the latter. Dr. Davy explained the effect of the neutral salts in brightening the blood on the principle of their producing a separation among the red particles. *Researches*, &c. vol. ii, p. 176 and 178. R. W.]

342 That aortic blood must contain rather less water than pulmo-arterial blood, is made probable, *a priori*, by the fact of the watery vapour which is always given off in the expired air. Direct experiment has confirmed this suspicion. Prevost and Dumas always found the dark coloured blood of the right side of

consistent coagulum than venous blood. But whether these differences depend on respiration or on another cause, is yet unascertain-

the heart to contain more water than the bright coloured blood of the left side, as the following Table makes manifest :—

	Blood of the pulmonary artery, (venous blood.)		Blood of the pulmonary veins or aorta (arterial blood).	
	Solids.	Water.	Solids.	Water.
Sheep (Ewe ?)	16,36	83,04	17,07	82,93
Cat . . .	17,41	82,59	17,65	82,35
	19,08	80,92	19,62	79,38
Sheep (Wether)	16,36	83,64	17,07	82,93

Lecanu found the same relations in the horse, in arterial blood : solids, 216,17; water, 783,83; in venous blood : solids, 204,320, water, 795,679. In another experiment the same inquirer found in arterial blood : solids, 214,5 ; water, 785,5 ; in venous blood: solids, 195,45; water, 804,55. (Lecanu, *Etudes chimiques sur le Sang*, *p.* 77.) Denis and others, on the contrary, could detect no determinate difference, in respect of watery and solid constituents, between arterial and venous blood. [The inquiries of Dr. John Davy,—one of the most accurate observers and conscientious recorders of facts that ever lived—deserve, nay require particular mention in this place, for I cannot myself help regarding this question of the relative proportion of water and of solid ingredients in the out-going and in-coming currents of blood as one of the most important in physiology. The experiments of Prevost and Dumas must have been made on the blood of the right and left sides of the heart, and the results they state are such as might have been expected : the blood entering the right side of the heart has just received the whole of the supply of water which is to be employed in the varied processes of the economy, almost every one of which implies the expenditure of some portion of this fluid; the very first operation to which the blood in commencing its circuit is subjected—exposure in the lungs—robs it on an average of some sixteen or seventeen ounces of water in the course of the four-and-twenty hours, and the returning current, the bright coloured but venous blood with reference to the lesser circulation, must contain this amount of water less than the out-going stream, here the darker but arterial blood. The proportions of watery and solid constituents in the two kinds of blood belonging to the systemic circulation, stand in the same relation to one another as they do in the pulmonic : the out-going stream is the more watery, the in-coming stream the more dense up to the moment of its being joined by the thoracic duct,—THE RETURNING CURRENT OF BLOOD IS INVARIABLY THE MORE DENSE. The blood of the aorta, in fact, begins to lose water almost immediately, and it is quite obvious that the stream which has supplied the watery elements of the urine and the perspiration, as well sensible as insensible, in particular, must be robbed of water by the whole amount of that fluid which these excretions contain: the blood which passes

ed[343]. Whether there be any difference in the temperature of arterial and venous blood is a point not yet quite settled among observers:

through the emulgent veins in the course of twenty-four hours, must contain from 40 to 60 ounces of water less than the blood of the emulgent arteries; for this is the quantity of urine daily discharged; the capillary veins of the skin must transmit on an average about 33 ounces of water less than the capillary arteries which feed the sudoriparous glands, for 33 ounces are on an average the quantity of watery vapour eliminated daily by the skin. The excellent observations of Dr. John Davy are in complete accordance with these statements; on no occasion did he find the systemic venous blood of lower density than the arterial; on the contrary, the venous blood was almost uniformly of greater density than the arterial, as the following tabular view will make manifest:—

TABLE of the specific gravity of Blood, Venous and Arterial, extracted from Dr. Davy's *Physiological and Anatomical Researches*, vol. ii. p. 24.

Animal.	Age.	Arterial blood.	Venous blood.
Sheep		1050	1056
Do.	6 years	1057	1058
Do.	16 months	1049	1051
Do.	do.	1047	1050
Do.	3 years	1047	1051
Lamb	11 weeks	1052	1055
Do.	do.	1046	1057
Do.	do.	1054	1054
Do.	do.	1050	1053
Do.	do.	1047	1050
Ox		1058	1061
Calf		1040	1046
Dog		1048	1053
Mean of all the observations		1050	1053

For an explanation of the effects which these different densities of the blood exert on nutrition generally, and on secretion, see my Annotation to § 218—23. Chap. VI. R. W.]

[343] That arterial blood contains more fibrine than venous blood, seems to be a point very generally agreed upon by observers—Lecanu, Prevost and Dumas, Denis, Letellier, &c. The difference probably depends on some portion of the fibrine being separated in the capillaries, and employed for the purpose of nutri-

Irvine held that the two kinds of blood were of the same temperature (31° R. 101,8° F.); Krimer, Schwenker, Scudamore, Dr. Davy, [and Becquerel and Breschet,] found arterial blood from 1° to 4° F. higher than venous; and Cooper, Coleman, and Martin, on the contrary, found the arterial blood of lower temperature than the venous. Upon a variety of other important topics, such as the capacity for caloric of the two kinds of blood, their electricity, the relation of the coagulum to the serum, the density of the serum, [see Annot. 218, p. 265] &c., the statements of observers differ considerably, from which we may infer that in these respects there are no constant differences between the two kinds of blood[344]. According to several French chemists and physiologists—Prevost and Dumas, Denis, Lecanu, &c.,—arterial blood contains a larger quantity of blood-corpuscles than venous blood; but this idea is far from being proved; for we are yet without any ready or certain means of determining the quantity of corpuscles in a given measure of blood.

§ 181. The blood contains a variety of gases in solution. These,

tion; in many diseases, partieularly in inflammations, the separation of fibrine from the eapillary vessels is an objeet of immediate observation. Part of the lost fibrine is undoubtedly returned to the blood by the thoraeie duet; whether fibrine be formed in the lungs during respiration, perhaps by a ehange in the albumen, has not been demonstrated, though it has been suspeeted.

[344 The experiments requisite to demonstrate most of the points here mentioned are of the most delicate kind; so delieate that I eannot faney any one authorized to eonelude that there is no constant differenee in reference to each of them between venous and arterial blood. Every prineiple of analogy would lead us to infer that there was a differenee, variable, probably, as between the arterial and venous blood of one animal and another, eonstant, as between the venous and arterial blood of the same animal. The observations of Dr. Davy, indeed, to seleet one point, show most elearly that in sheep and lambs, the blood of the earotid artery is of higher temperature than the blood of the jugular vein, and that in the same animals the blood of the left ventriele is warmer than the blood of the right ventriele, a eonelusion that has been eonfirmed by the very reeent experiments of Messieurs Beequerel and Bresehet. The opposite result obtained by Coleman and Cooper Dr. Davy eannot aeeount for, unless on the supposition of its being eonneeted with the mode in whieh the animals they experimented on were killed, namely, by asphyxia; for in many instances he found that, when the right ventriele was distended with blood (as it generally is in asphyxia) there was but little differenee of temperature between the two sides of the heart. *Researches, Physiol. and Anat.* vol. i, p. 147 et seq. and 211 et seq. R. W.]

as Magnus has shown, are oxygen, azote and carbonic acid. The absolute quantity of these gases which circulate dissolved in the blood has not yet been accurately ascertained, for they are expelled from it only with extreme difficulty; it would however appear to be considerable; the quantity of carbonic acid alone may sometimes amount to $\frac{1}{5}$th of the volume of the blood. The two kinds of blood are essentially distinguished by the quantitative relations of the different gases which they severally contain. Arterial blood always contains more oxygen and less carbonic acid than venous blood; venous blood, on the contrary, more carbonic acid and less oxygen than arterial blood. The azote appears to be in equal quantity in both kinds of blood[345].

[345] These conclusions are prineipally based upon the excellent experiments of Magnus (Poggendorff's *Annalen*, Bd. 40, S. 583), whose name is seeurity enough for their aceuracy. Earlier notices of the gaseous contents of the blood are extremely contradictory; Brande, A. Vogel and Davy, believed that they had extracted carbonic acid from the blood under the exhausted receiver of the air-pump; Hoffmann and Stevens found that venous blood shaken up with hydrogen gave off carbonic acid, and W. Bisehoff ascertained that the blood contained carbonic acid in the shape of gas. According to other excellent chemists, on the contrary—Dr. John Davy, Mitscherlich, Tiedcmann and Gmclin—no gaseous fluid was given off by the blood whether it was exposcd to heat, or placed under the exhausted receiver of an air-pump. The eommon and prevalent opinion now therefore came to be, that the blood in general eontained no gases in appreciable quantity. But Magnus demonstrated that the blood always contained gases, which could both be driven off from it by the agency of other gases, and extracted by means of the air-pump. He has also given a plausible explanation of the reason why the experiments of the chemists last mentioned gave a negative result: exposed to heat the albumen of the blood eoagulates, entangles the air, and so hinders its eseape; and under the air-pump the gases of the blood do not begin to escape until the column of mercury has sunk under an inch in height. In his experiments Magnus obtained the following results, which, for the sake of rendering comparison more easy, I have reduced to per centages.

1. The blood of a horse:

	Arterial blood contained 7,8 per cent of its volumc of gases; these consisted of	Venous blood, contained of gases a) 6 per cent.	b) 7,3 per eent.
Carbonic acid	55,1	72,1	70,4
Oxygen	19,3	18,9	17,6
Azote	25,6	9,0	12,0
	100,0	100,0	100,0

Final effects of Respiration—Theory of Respiration.

§ 182. After having considered the various changes that take place in the blood and in the air during respiration, we now ask what happens in the course of the respiratory process? This question we shall answer, in so far as it can be answered in the present state of our knowledge, without reference to the numerous hypotheses that have been broached in connection with the theory of respiration, and which have for the most part been definitively set aside[346]. The

2. The blood of another very aged but healthy horse contained:

	Arterial.		Venous.
	1) 12,5 per cent. gases.	2) 8,3 per cent. gases	11,1 per cent. gases.
Carb. acid	65,6	68,6	65,6
Oxygen	25,2	21,6	13,2
Azote	9,2	9,8	21,2
	100,0	100,0	100,0

3. The blood of a calf contained:

Arterial.		Venous.	
1) 11,8 per cent. gases.	2) 11,7 per cent.	1) 8,7 per cent.	2) 5,5 per cent.
64,8	55,5	76,7	79,3
24,1	23,8	13,5	12,9
11,1	20,7	9,8	7,8
100,0	100,0	100,0	100,0

These results exhibit nothing like a complete accordance, which, however, was hardly to be expected; for it is impossible to extract the whole of the gases from the blood; but it is quite certain that the relative quantity of oxygen to that of carbonic acid is regularly greatest in arterial blood. [Using an air-pump of great excellence, and constructed especially for the purpose, Dr. Davy has recently satisfied himself, in spite of a pre-existing bias, that gas is frequently though not invariably disengaged both from venous and arterial blood *in vacuo*. *Researches*, *Physiol. and Anat.* vol. ii, p. 153 et seq. R. W.]

346 It may not be amiss briefly to recapitulate the principal views which have been entertained with regard to the processes occurring in respiration, although they are now only of consequence as matters of history. Davy conceived that the carbonic acid evolved in respiration was formed in the lungs, the oxygen of the inspired air combining with the carboniferous element of the blood, which

venous or dark coloured blood which is thrown into the lungs contains certain gases in solution, consisting of a large proportion of carbonic acid, a little oxygen, and less azote. In the lungs the blood is brought into mediate contact with the air, and in conformity with the physical laws that regulate the absorption or penetration of the gases, it gives off a portion of its carbonic acid gas, and instead of this absorbs a portion of atmospheric air, or as it appears, of the oxygenous element of this in particular. Simultaneously with this exchange of its gaseous contents, the blood alters the dark red for the bright red colour, in virtue of some not yet thoroughly understood process; it may be in consequence of the simple absorption of oxygen, it may be in consequence of a chemi-

the blood-corpuscles were held to be. But when it was found that rather more oxygen was absorbed than there was carbonic acid evolved, this view was modified, and it was now maintained either that the superfluous oxygen united with hydrogen in the blood and formed water, or remained in combination with the blood-corpuscles. These are the views that have been currently entertained most recently. According to the old notions of Lavoisier, which were adopted by Prout, the blood gave off carbon and hydrogen, which combined with the oxygen of the air in the cells of the lungs, and so becoming carbonic acid and water, were expelled. Tiedemann and Gmelin, and Mitscherlich, held that venous blood contained a larger quantity of the carbonates than arterial blood, and they imagined that some portion of these carbonates, decomposed by the acetic [lactic] acid, which they believed to be produced during respiration, gave rise to the carbonic acid of the expired air. All these theories had of course to be abandoned when it was ascertained that venous blood contained free carbonic acid, and arterial blood, on the contrary, free oxygen, in its constitution, and that the quantity of carbonic acid present in venous blood, a certain measure of which in harmony with universal physical laws must be separated during respiration, was also competent to account for the whole of that which appeared in the expired air. Now Magnus has demonstrated the whole of these facts satisfactorily (Poggendorff's *Annalen*, B. 40). In a minute the quantity of carbonic acid gas expired by a man amounts, on the highest estimate, to about 13 cubic inches. In the same time from 5 to 10 pounds of blood pass through the lungs; consequently every pound of blood must give off from 1,3 to 2,6 cubic inches of carbonic acid gas. But we know that venous blood contains at least one-fifth of its bulk of carbonic acid; a pound of blood, consequently, which measures about 25 cubic inches, must contain at least 5 cubic inches of carbonic acid; each pound of blood circulating through the lungs, therefore, has only to part with from 1,3 to 2,6 cubic inches of carbonic acid in changing from venous into arterial, which it will readily do, in order to afford the whole of the carbonic acid that makes its appearance in the expired air.

cal combination occurring between this and the colouring matter. The blood loses farther a portion of its watery contents in the lungs, which are exhaled in the form of vapour dissolved in the comparitively drier air inspired. But in its principal constituents—in their quality, in their quantity, with the single exception of the colouring matter—the blood in its passage through the lungs suffers no essential change; it only loses a portion of the carbonic acid gas, which it had probably acquired in the capillary vessels, and in place of this absorbs a certain proportion of oxygen (and of azote?) which is in its turn exchanged in the capillaries by some process that has hitherto escaped our scrutiny, for carbonic acid. The lungs do not therefore appear to be as they have so commonly been held, the source and centre of animal heat.

CHAPTER V.

Of Secretion.

Preliminary Considerations.

§ 183. That portion of the blood which is distributed to all parts of the body to supply elements for their growth or maintenance, and which still remains within the circuit of the circulation, or returns to this again by means of the veins and lymphatics, is altered in a variety of ways, and some of its elements are separated in peculiar organs. The organs by which such separations are effected are called *secreting organs*, and the matters separated are spoken of as *secreted fluids*, or simply as *secretions*. A distinction has been made between those secretions that are produced with an ulterior view, as means to other functions of the economy, such for example as the saliva, the gastric juice, the seminal fluid, &c., and those that are immediately rejected from the organism, no farther use being made of them, such for example as the urine, the perspiration, &c. Fluids of the first kind are regarded more peculiarly as secretions, and are so designated; those of the second kind, again, are very commonly spoken of as *excretions*[347].

[347] The distinction between secretion and excretion has also been imagined differently. Müller, for instance, applied the title *excretion* in cases where the

Varieties of Form in which Secreting Organs present themselves.

§ 184. In their simplest forms the secreting organs of animals are structures composed of cells or fibres (modified cells), on the outer surface of which blood-vessels expand, and through the parietes of which fluids transude, penetrate the parenchyma, there undergo change, and distil from the side of the membrane opposite to that on which the blood-vessels ramify, in the shape of peculiar products. In general, however, secreting organs are not constructed so simply; the membranous layer or proper parenchyma thickens, consists of a multiplicity of layers of cells, undergoes inversion, and forms blind sacs, canals, and vesicles, associated in the most divers ways, generally clustered together and connected into particular compact organs by means of the blood-vessels which are distributed to them, and the cellular membrane, which penetrates everywhere. In these circumstances the secreting organ is called a *gland*, or, in contradistinction to the bodies of glandular structure, but which

constituents as such were already present in the blood, and have only been separated from it by the appropriate organs. To this division he refers urine and perspiration. The word *secretion*, again, he uses in cases where matters are prepared which cannot be supposed to be separated from the blood, in as much as they did not exist there previously, but which must be engendered from the proximate principles of this fluid by a chemical process—such fluids as the bile, the milk, the semen, for example. Vide his *Physiology* by Baly, vol. i. p. 429. This determination of the meanings to be attached to the words *secretion* and *excretion* would be excellent, were the premises upon which it is founded indisputable. But this is very far from being the case. Urea was long sought for in vain by chemists in normal blood, until it was very lately discovered by Marchand (vide § 100); it had hitherto been a question, therefore, whether urea was not a compound produced by the kidney. We know for certain, indeed, that a large quantity of urea is present in the blood after the extirpation of the kidneys. [The same thing occurs also in cases of a peculiar class of diseases of these organs—in granular degeneration, in the altered kidney that follows scarlatina, and in ischuria renalis. The colouring matter of the bile at all events is not formed in the liver; for we have evidence of its constant presence in the blood in the phenomena that accompany the disappearance of the effused blood in every case of simple bruise; and the worst form of jaundice is not that in which the biliary ducts are obstructed, but that in which the gall ducts contain no bile, the liver, struck with paralysis apparently, having ceased entirely from its secreting function, the consequence of which is, an accumulation of the elements of the bile within the system, and death by poisoning. Bile I hold to be just as certainly as urea one of the products of the chemistry which goes on in every part of the living body; the liver is merely the organ with which the elements of bile are in relation and by which they are eliminated. R. W.]

have no excretory duct, and are named blood-glands[348], it is designated a *secreting gland*[349]; in general it is spoken of merely as a gland.

§ 185. In the most comprehensive sense of the expression, the cellular membrane might be regarded as the simplest and most widely spread secreting organ of the body; for it is undoubtedly an organ in which certain separations from the blood, such as pigment and fat, take place. But the cellular tissue is, in fact, no more than the bond of union between the peripheral vascular system and the efficient tissues of the secreting organs. The fluids and matters which we sometimes observe contained within its interstices are always connected with pathological conditions, *e. g.* the infiltration of albuminous fluid, which occurs in dropsies, &c. The fat and pigmentary cells are properly neither mere deposited matters nor true secreting organs; but rather simple cellular produc-

348 Among the blood-glands are reckoned the spleen, thymus, thyroid and supra-renal capsules, the functions of which are unknown. They consist of a peculiar substance, or parenchyma, and numerous blood-vessels. In all probability they produce some change in the constitution or composition of the blood distributed to them, they appear one and all to be only of subordinate importance in the animal economy, as has been already stated in regard to the spleen in particular (§ 142). The thymus attains its highest development during the earliest period of infancy, or during the suckling; and from this time forward it begins to shrink till it disappears more or less completely about the age of puberty. [According to Mr. Gulliver's observations, the pulp of the supra-renal glands is chiefly composed of most minute oil-like molecules, which may be true nucleoli ready to be carried into the circulation, and such molecules he has actually sometimes found in the blood of the supra-renal vein, which he accordingly supposes may serve as the efferent duct of the gland. The thymus he regards as a special organ for the elaboration of nutrient matter in an appropriate shape to meet the wants of the economy at the precise time when these wants are most urgent. His conclusions tend to confirm the views of Hewson, so long and undeservedly neglected (see Annot. 198, p. 250). Mr. Gulliver's observations are by far the most complete and extensive we possess on the fluids of the thymus and supra-renal glands. Appendix to Gerber's *Anatomy*, where the subject is illustrated by figures. R. W.]

349 The principal work we possess on the form and structure of glands is that of Müller: *De Glandularum secernentium structura penitiori earumque prima formatione in homine atque animalibus*, c. tab. xvii. fol. Lips. 1830. In this work, in the subject of which the author had few predecessors of any note save Weber, Huschke and Rathke, the anatomy of the glandular system is exhausted in all essential particulars. Up to the time of Müller's appearance, indeed, the minute anatomy of glands, their elementary constitution of cells, &c., could not be successfully approached; science was not till then in a condition to grapple with these subjects.

tions, developed in harmony with the general scheme of cellular formations,—simple molecules are first deposited, which, serving as nuclei of future cells, throw out their envelopes, and subsequently become filled with peculiar matters abstracted from the blood. The fat which is contained in the fat-cells is also regarded as a deposit from the blood, which, under certain relations, is redissolved and taken up into the blood again, and so like a magazine of nutrient matter can be reapplied to form new combinations, and to serve other purposes in the economy[350].

§ 186. The serous and mucous membranes, and the external skin, have been regarded as secreting textures. To the serous membranes belong the pleuræ, pericardium, peritoneum, tunica vaginalis testis, tunica arachnoidea of the brain and spinal cord, and the synovial membranes. These are all formed of interwoven fascicles of cellular substance, and are covered on the free surface with a simple or multiple layer of tessellated epithelium. They are smooth moist membranes, readily permeable by the serum of the blood, which accumulating in extraordinary quantity within their cavities constitutes effusions or dropsies there ; in the normal condition however they seem to separate neither a fluid nor a halitus, or at all events to pour out either of these in very small quantity only. They are perhaps therefore improperly reckoned among the number of secreting organs[351]. The secreting apparatus of the mucous

[350] On the structure of the fat and pigmentary cells, see § 86, and also, as the newest and best work on the anatomy of the tissues, the *Allgemeine Anatomie der Menschen und Haussäugethiere*,—" *The General Anatomy of Man and the Domestic Mammalia*" of Gerber, edited with an Appendix by Geo. Gulliver, F.R.S. 8vo. Lond. 1841. See farther on the physiologically very remarkable contractile pigmentary cells of sepia octopus and the cephalapoda in general, my *Icones Zootomicæ*, Tab. xxix.

[351] If the serous membranes are not in the normal state, properly secreting, and if the mucous membranes be regarded as mere investments of internal cavities, in the same sense as the epidermis is an investment of the proper skin [or as the true skin itself is of the body at large] then are these membranes no secreting organs in the true meaning of the phrase, and actually secerning structures are all referable to the category of glands. It must be allowed, however, that a small quantity of fluid is very generally found in the serous cavities of recently slaughtered animals, for example in the pericardium, and occasionally also in the lateral ventricles of the brain. [Even this consideration ought not, I apprehend, to induce us to place the serous membranes at large among the proper secreting organs ; the fluids of all glands are peculiar, and different from the serum of the blood ; the fluids found in the serous cavities are mere serum ; they

membranes and external integument is not so much superficially extended and general, as it is concentrated into points and attached to an infinity of minute depressions, which lead to cavities that are either simple or ramified, and that consequently pass into the order of compound glands[352]; these are the mucous follicles and crypts, the sebaceous and the sudoriparous glands. These depressions or cavities are always covered with a multiple layer of epithelium, sometimes of the kind called tessellate, sometimes of that which is entitled cylindracious; crypts are always covered with tessellate epithelium, and the mucous or unctuous secretion of their cavities is regularly mingled with innumerable normal and altered epithelial cells, so that these may be regarded as regular constituents of mucus.

Structure of Glands.

§ 187. The type or elementary form of every secreting gland is either a simple capsule, an elongated blind sac, or a rounded vesicle,

are the effect of transudation of the coats of the vessels and the membranes, and not of any process akin to that by which bile or saliva or urine is formed. R. W.]

The same fundamental type is observed in the structure of the simplest follicle and of the most complex parenchymatous gland, which last, however, is to be regarded much less as an inverted membrane, than as a branched tube, or hollow tree divided from trunk to bough, and branch, and twig, and leaf, the walls of which are formed of variously shaped, often compact and angular or rounded, more rarely elongated and filamentous cells, like the brick-work or masonry of a dwelling-house. The lungs alone can be viewed in this sense as a membrane which has undergone inversion into itself. But the principle, that in the glands is realized the tendency within the smallest possible space, to have the greatest extent of secreting surface, loses nothing of its universality here. The aqueous humour of the eye might be regarded as a secreted product of the serous membrane which lines the anterior chamber of the eye; but there is no complete parallel between this and the rest of the secretions. [The external skin in itself is very certainly not a secreting membrane, but a membrane inclosing in its substance an infinite number of special secreting organs. The mucous membranes I believe to be essentially the same in structure. The serous membranes I view differently. Here I believe the lymphatic system to constitute the true secreting element in the tissue: *the serous membranes are, in the main, contrivances for the accommodation of a vast number of lymphatic vessels*, and for a purpose which I have exposed at length elsewhere. R. W.]

[352] It is very questionable whether the mucus of the mucous membranes is not always the product of the simple or compound follicles of these textures; it is even improbable that the superficially extended muco-membranous layers, those especially that are covered on the surface with a ciliate epithelium, should secrete mucus. To determine this question, however, additional researches are necessary.

upon the outer aspect of which vessels are ramified, and which on the inside generally exhibits numbers of small cellular projections or depressions, and an outlet through which the matter secreted escapes[353]. Many of the cutaneous and mucous glands, as also the simple glands of the stomachs of birds (Fig. CLXXII. B. *a d*), and the Lieberkühnian glands of the intestines, afford examples in point; but they soon begin to get more complex, coalescing, dividing,

[353] The principal forms of glands are exhibited in the tissues referred to in § 187—197, which comprise a careful selection of examples wherein the chief relations of their external forms and internal structures are displayed, every thin g like unnecessary detail having been avoided.

Fig. CLXXXVII.

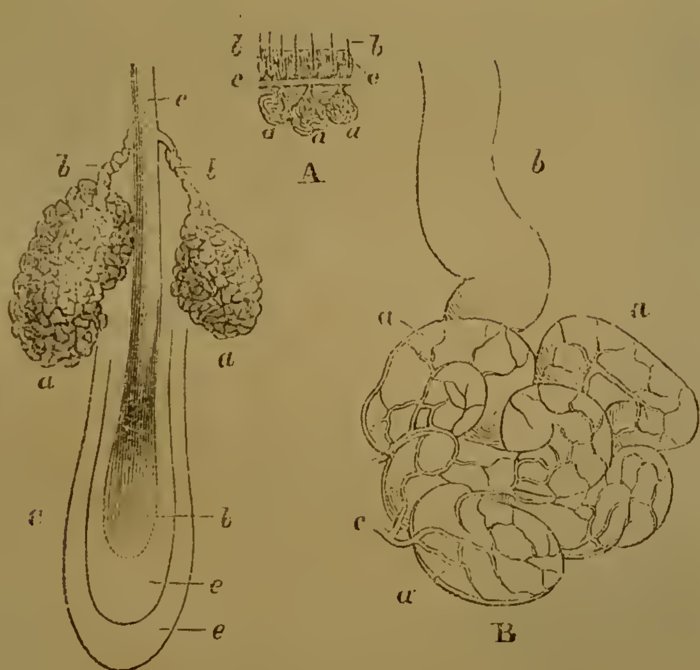


Fig. CLXXXVII. Glands from the meatus auditorius externus of a young female of 18. A, Section of the skin; seen magnified three diameters; *b*, *b*, hairs; *c*, *c*, superficially situated sebaceous glands; *a*, *a*, larger and more deeply seated glands which are coloured yellow, and appear to secrete the cerumen. B, A gland of this kind more highly magnified. *a*, *a*, the tortuous canal composing the gland and passing over into the excretory duct *b*; *c*, a small vessel with its branches. C, a hair of the auditory passage, penetrating the epidermis at *c*, and at *d*, contained within its double follicle *e*, *e*; *a*, *a*, sebaceous follicles of the hair with their excretory ducts.

sending forth new lateral lobules (Fig. CLXXII. B. *e* and fig. CLXIX. A. B), and by repetitions of the same process even acquiring

Fig. CLXXXVIII

Fig. CLXXXVIII. Sudoriparous gland from the palm of the hand of a young person 18 years of age. A, a gland entire with its excretory duct, magnified 40 times; *a a*, the convoluted canals that form the gland, and from which two excretory ducts arise, *b*, *b*, which unite to form the single spiral duct, which at *c*, passes through the laminæ of the epidermis, and opens on the surface at *d*; *c*, *c*, surrounding fat-cells. B, the same gland more highly magnified. Around the canal of the gland play the vessels, *b*, *b*. C, a few fat-globules from the emptied fat-cells.

a pretty complicated mulberry appearance (Fig. CLXXII. B. *f*,). The ventricular glands of mammals are already somewhat more compound (Figs. CLXVII. et seq). The extent of secreting surface can be increased without any additional external complexity, by a capsule or canal extended in length, and at the same time rolled up or convoluted upon itself. We have an example of this kind of gland

CLXXXIX.

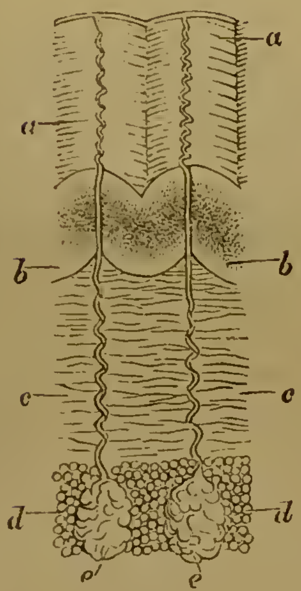


Fig. CLXXXIX. Two sudoriparous glands after Gurlt, *Magaz. f. d. gesammte Thierheilk.* 1835, Tab. 2 fig. 1. *a*, epidermis; *b*, tactile papillæ; *c*, corium; *d*, adipose tissue; *e*, sudoriparous glands.

FIG. CXC.

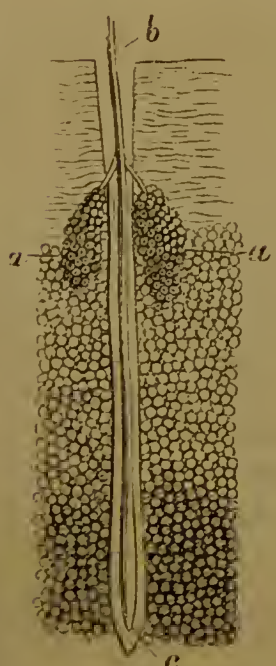


Fig. CXC. A thin layer from the scalp of the human subject. *a*, *a*, sebaceous glands; *b*, a hair with its follicle, *c*. After Gurlt, *Mag. f. d. gesam. Thierheilkunde*, 1835.

in the ceruminous glands of the ear (Fig. CLXXXVII. A. B)[354], and in the sudoriparous glands (Fig. CLXXXVIII. A. B.). We have only to conceive these two forms farther subdivided, ramified, and the several parts connected by means of vessels and cellular tissue, to have a perfect idea of the most complex parenchymatous gland. The skeleton of every gland is the ramified excretory duct, formed in the manner already described, to which are attached the secreting blind sacs, vesicles, or tubes, connected together by cellular tissue, and surrounded by net-works of capillary vessels[355].

§ 188. The best picture we possess of the vast variety that exists in the structural connection of the several parts of the glandular skeleton, is in the secreting organs of insects, particularly the salivary glands (Fig. CXCI.) and the testes. Here we observe the most elegant and singular forms, having frequently much of the vegetable character in their appearance. The salivary glands pre-

[354] This is the first time that this organ has been figured. The ceruminous glands have a yellow colour, and measure from one third to one half a line in diameter.

[355] I find the sudoriparous glands somewhat different in their structure from what they were believed to be by the original observers. Purkinje and Wendt, for example, describe and figure them as simple saclets (Müller's *Archiv*, 1834, tab. iv.) ; Gurlt saw them as convoluted canals (*Ibid.* 1835, S. 416, tab. x.) ; and his figure is here copied (Fig. CLXXXIX.) to contrast with the structure as I have observed it. I find the sudoriparous gland to consist of a convoluted canal still more distinctly than Gurlt's figure exhibits it ; and occasionally (or generally ?) with intermediate excretory ducts (Fig. CLXXXVIII. A, *b*, *b*) ; or may it be a double or divided canal ? Such at least was the appearance presented on two different occasions in perfectly recent bodies, the one of a man, the other of a woman, in which I examined the structures in question. The sudoriparous glands measured from $\frac{1}{4}$th to $\frac{1}{5}$th of a line in diameter, and were visible to the naked eye as minute points. The glandular canal was $\frac{1}{8}$th, the spiral excretory duct $\frac{1}{100}$th, of a line in diameter. I find it best to take a very fine slice by means of the double-knife contrived by Valentin, from a piece of fresh skin out of the hollow of the hand, to place this immediately under the microscope, and to make gentle pressure upon it. All artificial means of hardening the integument, such as solutions of carbonate of potash, &c., I found to be disadvantageous rather than serviceable. [The structure of the sebaceous glands of the skin (Fig. CLXXXVII. C, *a a*, and CXC. *a a*,) is very different from that of the sweat glands. Instead of being a convoluted canal the secreting organ here is an aggregation of vesicles, and the ducts instead of ending independently on the surface of the skin, seem always to terminate in the sheaths of the hairs. R. W.]

sent themselves now as filiform canals (Fig. CXCI. B), now thicker and convoluted, now with a sacculate end (C), here extending into a simple (E) or a double vesicle (M), there branched like the horns of a deer (G), or in the guise of a pair of long shaped canals ending

Fig. CXCI.

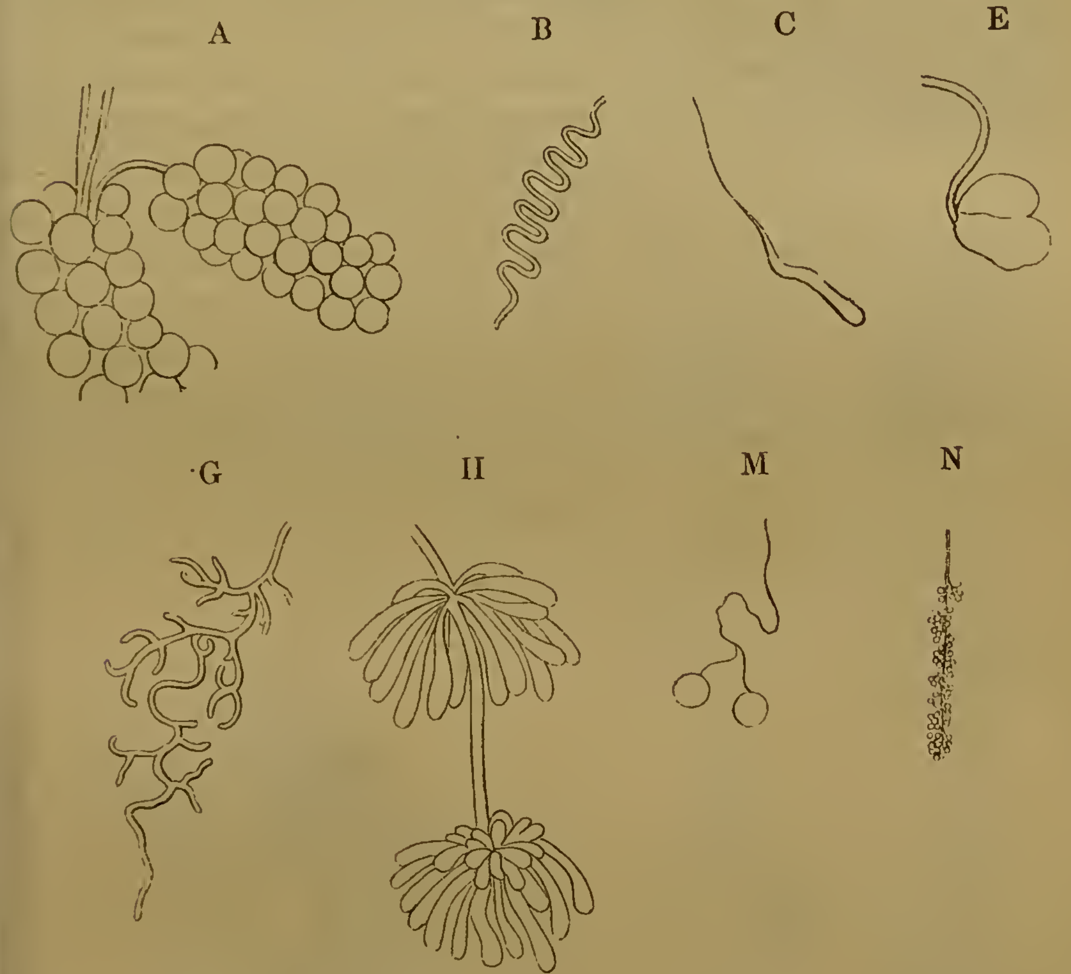


Fig. CXCI. Salivary glands of insects, to show the variety in the form and combination of the secreting follicles, from the simple lobular or filiform canal and blind sac to the greatly complicated raceme.

A. Part of the salivary gland of Nepa cinerea. After Ramdohr.

B. Salivary vessel of Asida grisea. After Succow, *Anat. physiolog. Unters.*

C. Salivary vessel of Musca deviens. After the same.

E. *The same* of Musca carnaria. After the same.

G. *The same* of Blaps gigas. After the same.

H. *The same* of Cicada ormi. After the same.

M. *The same* of Pulex irritans. After Ramdohr.

N. *The same* of Scolopendra Afra. After nature.

(All these figures, with the exception of that indicated by N, are more or less magnified).

in many smaller saccules, or forming a tuft or corymb of blind canals (H), or a cluster of vesicles connected like a bunch of grapes or berries to a common duct (A, N).

The varieties in form presented by the seminal organs or testicles are still greater, new inquiries constantly offering new shapes to our notice. From the simple, linear and filiform canal of Julus (Fig. CXCII. 1.), to the highly complicated yet beautiful appearance, comparable to a leafy tree laden with fruit, which we observe in Silpha obscura (Fig. CXCII. 10.), there are forms of every intermediate degree of complexity, but always as varieties of the same elementary type. Even the simple canalicular or sacculate form presents numerous variations. In one case it is the straight pretty regular canal already indicated (1); in another the canal is irregular, of different thicknesses in different parts, and tortuous (2); in a third it is spirally twisted (3), or is rolled up into a skein simple or double and with club-shaped ends (4), in every case for the obvious purpose

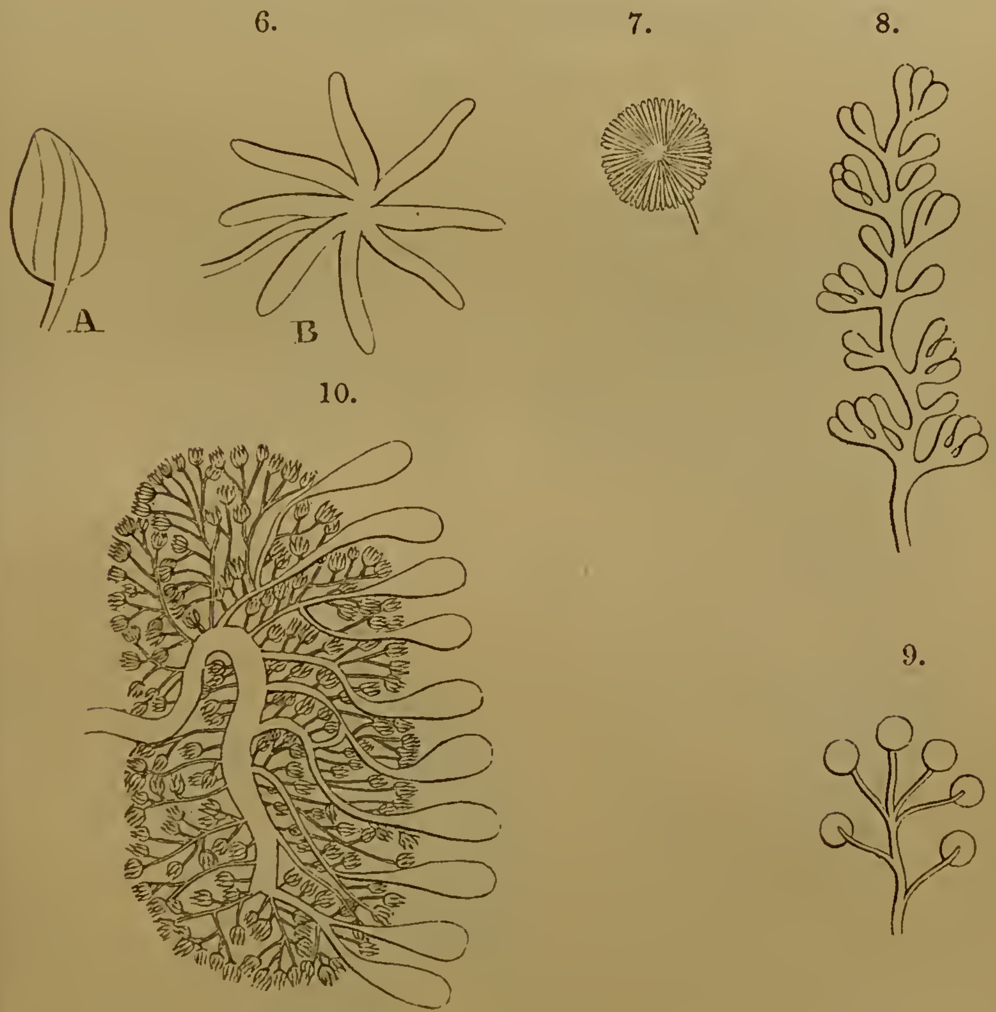
Fig. CXCII.

1. 2. 3. 4. 5.

1 Testis of Julus.
2. Tipula crocata.
3. Ranatra linearis.
4. Harpalus ruficornis.
5. Cercopis spumaria.

of saving room ; in other instances, still, the organ presents itself in the shape of one or more club-like canals nearly straight (5), or bent at an angle with commencing divisions at the end, or with the end forming a rounded vesicle; or otherwise two cœcal canals are connected like hooks, or they are finger-shaped, or they form tufts of different kinds—quiver-like, star-shaped (6), or like the flowers of syngenesious plants, (7), or they form small saccules in the shape of pannicles (8), or they are clustered like grapes or berries and attached to styles (9). In this way do the forms of this gland alter

Fig. CXCII. (Continued.)



6. Capsus tricolor.
7. Bostrichus capucinus.
8. Staphylinus maxillosus.
9. Prionus coriarius.
10. Silpha obscura.

Fig. CXCII. A view of some of the numerous forms presented by the testis or organ secreting the seminal fluid in the class of insects, after Leon Dufour, Succow, and Treviranus.

in nearly allied species in the insect world, so rich in varied forms[356]. The peculiar constitution and mode of distribution of the blood of the insect division of the animal kingdom (§ 111) probably required

[356] There are few divisions of the comparative anatomy so much calculated to set in a clear light the importance of this science in connection with the study of general morphology, as the sketch just given of the vast variety of form presented by the glandular system. If we would give plans or ideal outlines of the principal forms of the different elements of the glandular system in man and the more perfect animals, no better method could be followed than to pursue a single gland through the class of insects. As supplementary to this part of our subject, the elegant forms which the clustered canals and vesicles of others of the special secreting organs of insects exhibit may be referred to in the subjoined Figures.

Fig. CXCIII.

Fig. CXCIII. The glands of insects which secrete the acrid or corroding juice, after Leon Dufour, *An. d. Sc. Nat.* T. vii, pl. 19 and 20. A. Of Chlænius velutinus B, Of Brachinus crepitans. C, Of Calathus fulvipes.

the singular unfolding of the glandular elements which we observe among its members. The blind extremities of the glands are surrounded immediately by the blood, which is poured freely into all the interstices of the body, and so attract the substances from its mass which the glands of other and higher animals have brought to them by finely divided capillary reticulations, to be subjected to their peculiar elective attractions.

§ 189. It is infinitely more difficult to form an idea of the glandular skeleton of man and the vertebrata, in the fully formed condition, the composition of this being much obscured by the connecting cellular tissue and intermingled net-works of vessels. Still there are cases even here, where, without peculiar difficulty, the two principal types in glandular architecture may be seized. As examples, the Harderian glands of birds generally (Fig. CXCIV.)[357], and the Cow-

[357] I have selected two conglomerate glands as types which are readily procurable by all, and which can easily be filled with mercury in the most beautiful and perfect manner. The Harderian gland is a glandular body situated in the orbit, which occurs in birds and many mammals, for example, in the hare, and which is readily to be injected with quicksilver. In the goose the appearance presented is uncommonly beautiful. The body has been figured by Müller, *De Gland. structura*, Tab. v. figs. 6 and 7, in the goose and hare. I have chosen the Harderian gland of the pelican as the subject of my description and figure, partly

Fig. CXCIV.

A

B

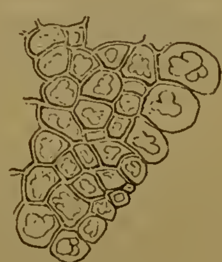


Fig. CXCIV. A. A Harderian gland of the Pelecanus onocrotalus, with the excretory duct of the natural size injected with mercury. B. A portion of the same slightly magnified. Some vascular ramifications are still apparent between the lobules.

per's glands of the hedgehog (Fig. CXCV.) may be quoted. Into both structures a quicksilver injection flows readily, and renders the arrangement of their parts perfectly distinct even to the naked eye. The gland of Harder of the pelican (Fig. CXCIV.) is seen as a considerable lobulated body, each lobe being subdivided into smaller rounded or elongated or angular lobules, which again present themselves as small hollow pannicles or berries, attached to the enlarged excretory duct, these in their turn having still smaller, rounded blind cells (Fig. CXCIV. B) surrounded by vascular net-works attached to them, an arrangement by which the whole structure acquires a cauliflower appearance. The Cowper's glands of the hedgehog, on the other hand, (Fig. CXCV. A) afford an example of that form in which the ramified excretory duct divides into elongated, pretty even, and slender cœca, which subdivide at their ends into finger-shaped processes (Fig. CXCV. B), partly straight, partly sinuous, which are then applied to one another in the form of flat lobules, these in their turn being connected by cellular tissue into larger lobes.

§ 190. In man and the higher vertebrata, glands of the simple follicular form (as they exist in the Lieberkühnian glands of the intestines, for example) attain to the highest degree of complexity —in the liver, for instance. The compound glands may be arranged according to their structure into four groups. 1. *Compound follicles*, the short excretory canal passing without farther ramifica-

that I might give a new representation of the body, and partly because it is here still larger, and the structure still more obvious. Compare also the figure of the Cowper's gland of the hedgehog, in Müller, l. c. Tab. iii. figs. 8 and 9, with that which I have here given.

CXCV.

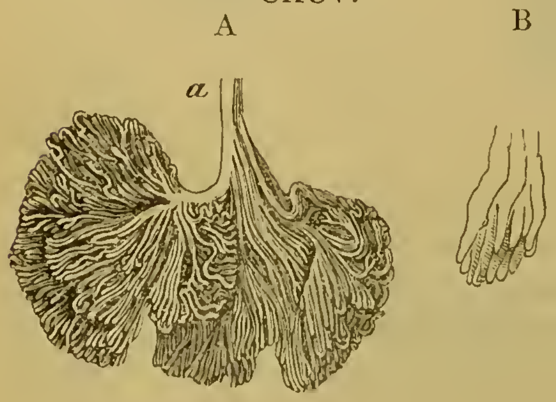


Fig. CXCV. A, the Cowper's gland of the hedge-hog with the excretory duct *a*. The cœca composing the gland are filled in the most beautiful manner with mercury; the object is not magnified. B, A few of the blind sacs seen slightly magnified.

tion at once into pediculated vesicles or racemiform lobules; or the outwardly simple sac exhibiting internally open cellular projections or shallow pits; to this head belong the greater number of the larger mucous and cutaneous glands. 2. *Glands with tree-like ramifications of their excretory duct*, and enlargements of the terminal branches into racemiform or cauliflower-like aggregated vesicles, which are visible with the naked eye, and vary in magnitude from the 25th of a line to 1 line. To this rubric belong the lachrymal glands, the salivary glands, and the pancreas. The lung of the mammal, with its terminal vesicles attached to the minute ramifications of the bronchi, may serve as prototype of this form of gland, which is made up of repetitions of the same fundamental structure, as we have seen in the preceding paragraph to be the case with regard to the Harderian gland. 3. *Glands with a tubular structure*; the secreting canals are here extremely slender, of great length, convoluted, blind at the ends, not ramified or only once or twice divided, not sensibly or but very slightly enlarged at the extremities, sometimes anastomosing by recurrent loops, or connected by cross branches, and from the 10th of a line to half a line in thickness; to this category belong the kidneys and the testicles especially. The Cowper's gland of the hedge-hog (Fig. CXCV.) may serve as prototype of the form of which that of the organs just mentioned may be viewed as an extension. 4. *Acinous glands*. The excretory duct here ramified through the substance of the gland, divides at length into extremely minute branches; all the branches and twigs are beset with compact lobules which consist of very small, firm, angular cells, which effect the secretion. To this division belongs the liver of vertebrate animals generally.

§ 191. Compound follicles or glands of the first description are progressive or more complex forms of the rounded or elongated inversion, which we have seen constituting the simple follicle of the mucous membrane and of the skin (§ 187); no precise line of demarcation can in fact be drawn between them and the simple follicle—the Lieberkühnian glandlet, for example—or the sudoriparous or ceruminous gland. The large glands of the stomach and intestines may serve as types of this kind of gland (Fig. CLXXI), or the numerous glands which are in connection with the skin—the

glands of the prepuce and nymphæ, for example[358]. All these glands consist of ramifications of the excretory ducts, which swell out into single saccules, that do not combine into true racemes or lobes. The glands which are connected with the hairs (Fig. CLXXXVII. C *a a*, and CXC. *a a*) are small follicles with rough external surfaces, and internally presenting the appearance of projecting parietal cells. To this division also belong the associated unbranched saccules, arranged along the excretory duct like the grains of an ear of barley, which compose the Meibomian glands[359]. Among animals a multitude of variously formed glands of the skin, other than the sudoriparous and sebaceous glands, are encountered[360].

§ 192. The progressive development of the last form of gland is observed in the lachrymal, salivary and lacteal glands[361], in all of

[358] The mucous glands of the nymphæ are figured by Wendt in his paper on the human epidermis in Müller's *Archiv.* 1834, Tab. iv.

[359] Figured by Müller—*De Gland. structura*, Tab. v. fig. 1 and 2.

[360] To this number belong, for example, the musk bag, which lies between the umbilicus and glans and opens into the prepuce, the inner aspect of which is marked by superficial depressions; and the anal sacs of many animals—the martyn, the otter, &c., which exhale a peculiar odour or stench, are of the same description. They are, in fact, extensive involutions of the skin, of simple structure, occupied internally by shallow pits; these structures might be regarded as simple follicles, which upon occasion, however, may become more complicated, as they do in the anal sac of the hyæna, for example, which is made up of several racemes clustered together.

[361] On the structure of the glands in general, and of each of those mentioned in particular, see the work of Müller, and the *Elementary Treatises on Anatomy* of E. H. Weber and of Krause.

Fig. CXCVI.

Fig. CXCVI. A very small piece of the parotid gland of a new-born infant, filled with mercury and magnified five diameters. After Weber.

which a greater amount of ramification, an increase in the quantity of vesicles and racemes produced, and a greater degree of separation of the individual parts into lobes, are observed. The lachrymal gland of man, of mammals and of birds, exhibits terminal cells, which in the latter creatures are large and conspicuous; in man, on the contrary, they are much smaller. The salivary glands of man are formed in the same way (Fig. CXCVI.) The cells of the terminal vesicles of the parotid may still be readily filled with mercury in young subjects; they are two or three times smaller than the finest pulmonary cells, measuring no more than from the 30th to the 60th of a line in diameter. The structure of the pancreas is similar, and the terminal vesicles of this gland are very easily filled with mercury or with air, in birds especially, measuring when thus distended from a 50th to a 30th of a line in diameter[362]. The mammary glands in the ornithorhynchus are extremely simple, and exhibit the commencement of a series of evolutions that end with the most complicated raceme: the structure here consists of a congeries of very large unramified cœca[363]; but in the higher mammalia and in man the wide excretory ducts pass over into finer branched canals, upon which the terminal cells form botryoidal clusters; the cells are on an average from $\frac{1}{20}$th to $\frac{1}{15}$th of a line in diameter.

§ 193. Among the glands having tubular vessel-like secreting canals, the KIDNEYS and the TESTES deserve particular notice. The development of the kidneys in the vertebral series is of especial interest. In fishes and amphibia the entire tissue of the kidney consists of tortuous canals, which end partly in blind extremities, and partly pass into one another in loops, but which, from their great length and intimate connection, cannot be demonstrated singly. They are not divided into single pyramids or lobules, a peculiarity

[362] The pancreas of fishes has been very commonly quoted as affording an example or type of the successive evolution of glands from the simplest cœcal tubes to the most complex form observed in the glandular system. Recent inquiries, however, rather lead us to conclude that the bony fishes in general have a pancreas which is comparable in all respects to that of the other vertebrate animals; perhaps the cœcal appendages which were so long mistaken for the pancreas have a totally different function.

[363] See Meckel: *Ornithorhynchi paradoxi descript. Anatom.* Tab. viii. [and Owen on the mammary gland of the Ornithorhynchus in *Philos. Trans.* R. W.]

that first makes its appearance among birds. Here the highly tortuous uriniferous tubules are furnished with lateral branches, which come off like the tines of a stag's horn; in all probability they pass over the one into the other by means of loops. In the mammalia the tubuli uriniferi form many pyramids or lobes (renculi), each a system by itself (Figs. CXCVII. and CXCVIII. A). In the cortical substance of the human kidney, the tubuli can be traced, although with difficulty, winding among the vascular plexuses or

Fig. CXCVII.

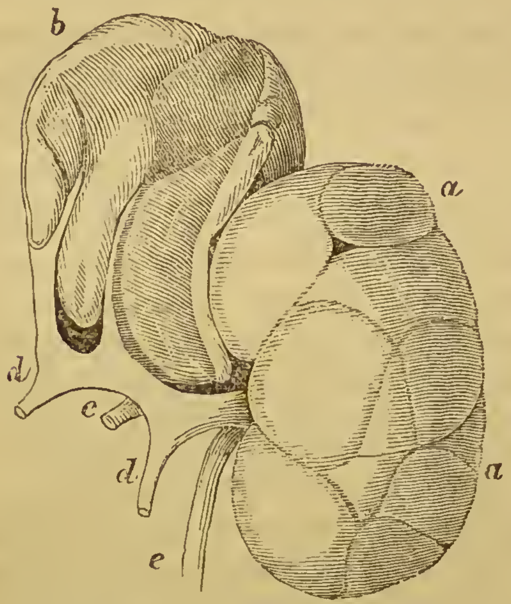


Fig. CXCVII. Kidney aud supra-renal gland of the new-born ehild, of the natural size. *a*, kidney; *b*, supra-renal gland; *c*, artery; *d*, veins; *e*, ureter.

Fig CXCVIII.

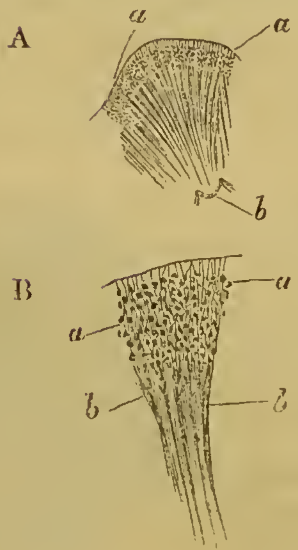


Fig. CXCVIII. A. B. Portions of the kidney represented in Fig. CXCVII injeeted. A, of the natural size; the Malpighian bodies, *a*, *a*, appearing as points in the eortical substanee; *b*, the papilla of one of the tubular pyramids. B, a small portion of A, seen under the simple lens and slightly magnified; *a*, Malpighian bodies; *b*, tubuli uriniferi.

skeins, mostly looped towards the margin of the organ and running into one another (Fig. CXCIX, *b*, *b*), or ending blindly, (a)

Fig. CXCIX.

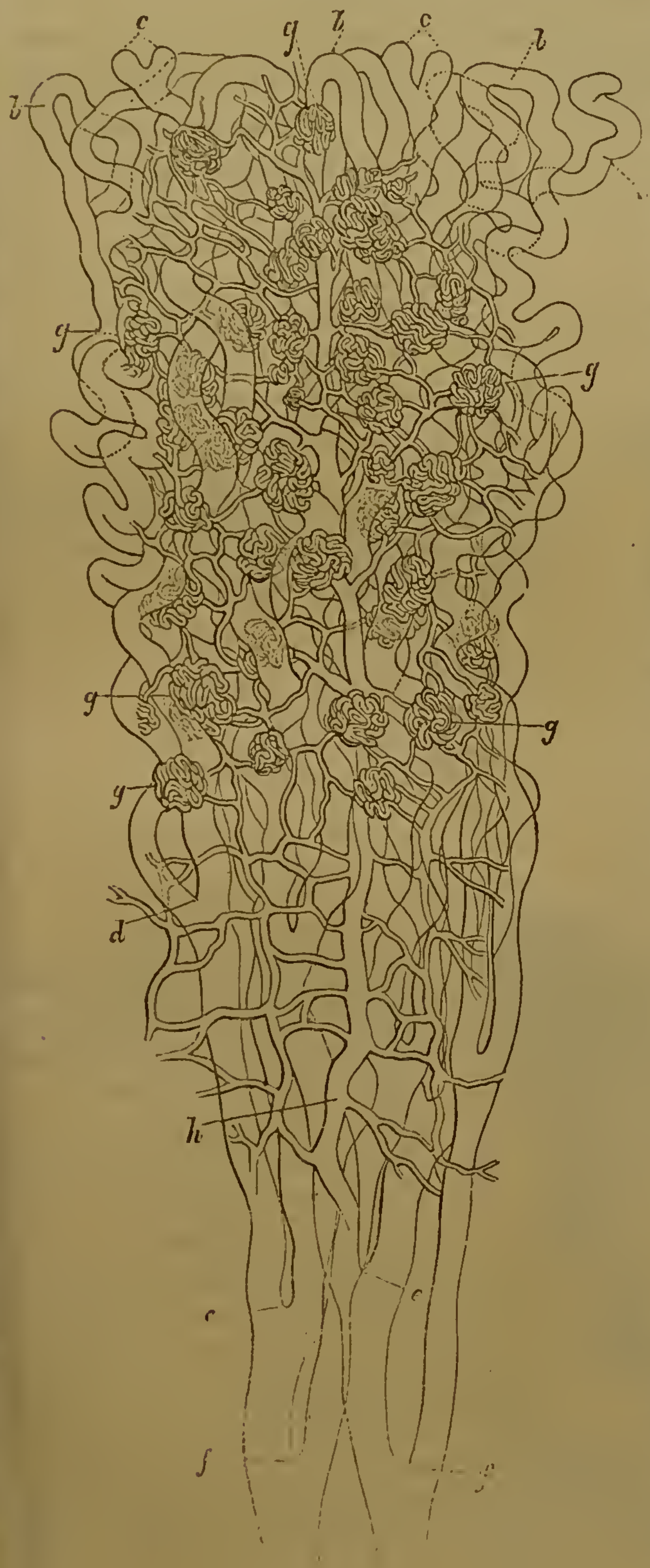


Fig. CXCIX. A still smaller piece of the same kidney magnified about 60 diameters and drawn in part as a plan, so that the relations of the tubuli to one another and to the vascular glomeruli may be distinctly seen and understood. *a*, a simple terminal tubulus uriniferus; *b*, *b*, tubuli, forming loops and returning; *c*, *c*, tubuli terminating in bifurcated points; *d*, *e*, *f*, points where the tubuli join, continuing their course towards the papilla; *g*, *g*, *g*, arterial glomerules or convolutions, connected with one another by a general vascular rete; *h*, a larger arterial trunk, which feeds this reté and the connected glomeruli (the Malpighian bodies).

Fig. CC.

Fig. CC. Termination of one of the tubuli uriniferi from the kidney of an adult, examined soon after death. The cellular structure is conspicuous. Magnified 250 times.

more rarely slightly enlarged and club-shaped, (Fig. CC.) occasionally also cleft (Fig. CXCIX. *c*). The entire cortical substance consists of convolutions of the uriniferous tubules, which are found to present a very nearly uniform diameter, and which on an average may be from about the 60th to the 50th of a line. They unite two and two as they approach the tubular or medullary structure, becoming at the same time somewhat thicker, and then they run quite parallel to one another to their termination (Fig. CCI)[364].

[364] Observers are not yet agreed in regard to the minuter structure of the

Fig. CCI.

Fig. CCI. A lobe of the kidney of the adult porpoise (Delphinus phocœna). After Müller.

Fig. CCII.

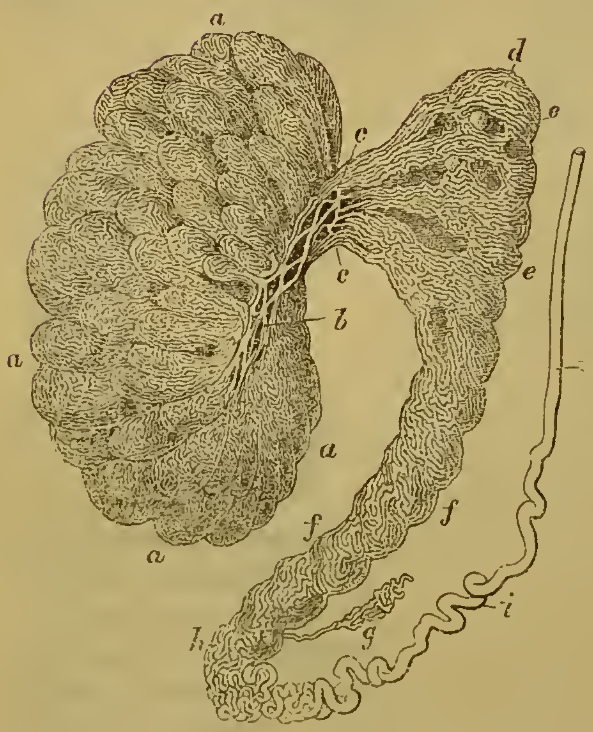


Fig. CCII. A human testis injected with mercury in as complete a manner as possible, after Lauth (*Mem. de la Societé d'hist. Nat. de Strasbourg*. T. i.) *a*, *a*, lobules formed by the most delicate tubuli semeniferi; *b*, reté testis; *c*. vasa efferentia; *d*, flexures of the efferent vessels passing into the head of the epididymis *e*, *e*; *f*, body of the epididymis; *g*, its appendix, and *h*, its tail; *i*, vas deferens.

§ 194. The structure of the testis has already been described (§ 26). Here the entire mass of tubuli seminiferi may be said to form but a single vessel having numerous anastomoses, the vessel however being of such excessive length that its convolutions form a vast number of lobules (Fig. CCII. *a*, *a*). Perfectly successful injections of the tubuli semeniferi with mercury are extremely rare, and the series of anastomoses can only be shown in a plan or diagram, such as Figure CCIII. The finest tubuli, *a*, *a*, which are about $\frac{1}{15}$th of a line in diameter, form an extensive network of

kidney; the above description is after my own researches. Krause has very lately given a careful description and representation of the structure as he saw it. Müller's *Archiv*, 1837, Tab. i. Besides anastomoses he found blind but not enlarged ends near the points of anastomosis.

Fig. CCIII

Fig. CCIII. Plan of the structure of the testis and epididymis and of the connections and course of the tubuli semeniferi (after Lauth). *a*, *a*, tubuli semeniferi and their anastomoses *a*,* *a**. The other references as in last figure.

vessels divided into lobules, and pour the fluid they have secreted into the *reté testis*, *b*, from which the vasa efferentia, *d*, *d*, take their rise, and these terminate in the head of the epididymis, *e*, *e*, or greatly convoluted excretory duct, which gradually becomes less and less wound upon itself, and forms the vas deferens. It is in the testis that the vessel-like form of the secreting glandular canal is most completely realised; we here see a very extensive secreting surface packed up in a truly wonderful manner within a very limited space; and it is not unworthy of remark that the structure, however intricate in appearance and difficult to be understood, is nevertheless one of extreme simplicity[365].

§ 195. Among the whole of the vertebrata the parts which are the efficient agents of secretion in the *liver* are so intimately connected into a compact and little lobular organ by means of the vessels and cellular substance, that it is extremely difficult to form a proper notion of its structure. Perhaps the following is the true account of the structure of the liver when fully formed in man and the mammalia: It is easy to obtain conviction of the fact that the ends of the secreting parts of the liver are leaf-like lobules with blunt projections, which in preparations of the organ are most apt to remain attached to the minute venous twigs (Fig. CCIV. A. *a*, and CCV. *a*, *b b*). These

[365] The very complete and excellent description of Lauth (*Mem. de Strasbourg*, T. i.) has been made the basis of the preceding short account of the structure of the testis. The testis of the mammiferous animal in general is constructed on precisely the same plan; in birds also and in the scaly amphibia the testis is a greatly convoluted vessel. In fishes and the naked amphibia a different type is followed. The comparison of the testis and its efferent duct in the cartilaginous fishes with those of man is very interesting. The secreting ends of the

Fig. CCIV.

Fig. CCIV. A. Four lobules from the liver of a human subject 40 years of age, magnified twice; a branch of the hepatic vein, *a*, receives a more minutely ramified twig from each lobule. B, Some of the cells of which the lobules of the liver are composed, seen under a magnifying power of 200; in the greater number the clear nucleus is apparent.

lobules are composed of compact angular and rounded cells (Fig. CCIV. B.) Betwixt the several divisions of the cells of the indi-

tube are here small round capsules, which lie within larger globular vesicles, and which serve instead of or seem to typify the lobules; from these arise vessels which form a reté, pass into vasa efferentia, which in their turn terminate in the epididymis, precisely as in man, save that they are spread out flat, so that here the natural arrangement is in all respects that of the diagram (Fig. CCIII), which Lauth has given of the human testis. See the representation of the male organs of generatiou in a shark in my *Icones Zootomicæ*, Tab. xxii.

FIG. CCV.

Fig. CCV. *a*, A branch of the hepatic vein with the tributary twigs of which the lobules of the liver are connected as leaves are with the final branches of a tree. The venous ramuscles (venæ intralobulares) lie in the middle of each lobule, as is seen in the two next succeeding figures which represent transverse sections of the hepatic lobules magnified. After Kiernan.

FIG. CCVI.

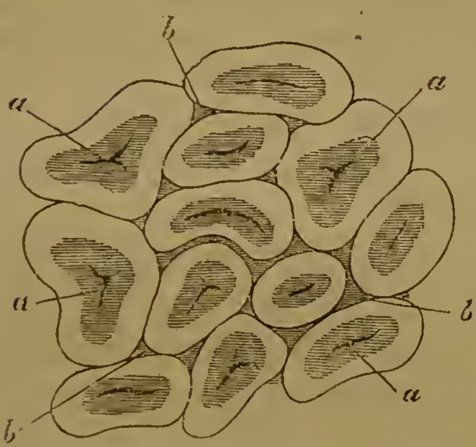


FIG. CCVI. Lobules of the liver, superficially situated, divided horizontally; *a a*, intralobular veins; *b b*, clefts between the several lobules, in which cellular tissue, minute subdivisions of the hepatic ducts, of the vena portæ and hepatic artery, are included; the middle portion of each lobule is here in a state of congestion. After Kiernan.

FIG CCVII.

Fig. CCVII. The intralobular plexus of biliary vessels, as figured by Kiernan—although the injection of these vessels was not so complete as it is here represented; *d*, *d*, two lobules divided across, with the ramifications of the hepatic vein, *a a*, the twigs of which perforate their centres; *b*, *b*, *b*, *b*, branches of the hepatic duct, as they take their rise from the plexus of biliary vessels which are here injected and surround the uninjected portion of the substance of the lobules *d*, *d*; *c*, cellular substance between the lobules.

vidual lobules, the branches of the gall-ducts penetrate (Fig. CCVII), and there form anastomosing retés, which surround single groups of cells like islets[366]. Some observers describe the final ends of the se-

366 The structure of the liver is so hard of discovery, and still continues surrounded by such obscurity, that every view which has yet been published leaves something of doubt upon the mind as to its perfect accuracy. That the acini are not thin-walled cells in the same sense as the blind ends of other glands, I hold for certain. They consist of a thick layer of angular cells, as stated above. That they are associated into lobules with blunted processes, and that these again are separated from one another by cellular tissue (Fig. CCVI.), seems to me equally certain. I find it much more difficult to say how the different vessels—the last subdivisions of the vena portæ, of the vena hepatica, and of the ductus hepaticus—comport themselves in the interior of the lobules. I regard the beautiful figures and the descriptions of Mr. Kiernan (*Philos. Trans.* 1833) as the best and most accurate that have yet been published, although they very certainly also include many mistakes. They agree in general with my own particular observations. But a very distinguished observer, Krause, combats the views of Kiernan, holding them for hypothetical. Krause succeeded with the assistance of the air-pump in filling blind terminal vesicles in the liver of the hedgehog with injection; he also filled the same vesicles partially with mercury, so that individual acini became visible with the naked eye on the surface of the liver. Krause in Müller's *Archiv*, 1837, S. 16. All my attempts to inject the liver of the hedgehog with mercury have hitherto failed. It is to be understood that when I speak of the *acinous* structure, and of the *acini* of the liver, I do not use the words in the same sense as Malpighi and the older anatomists.

Fig. CCVIII.

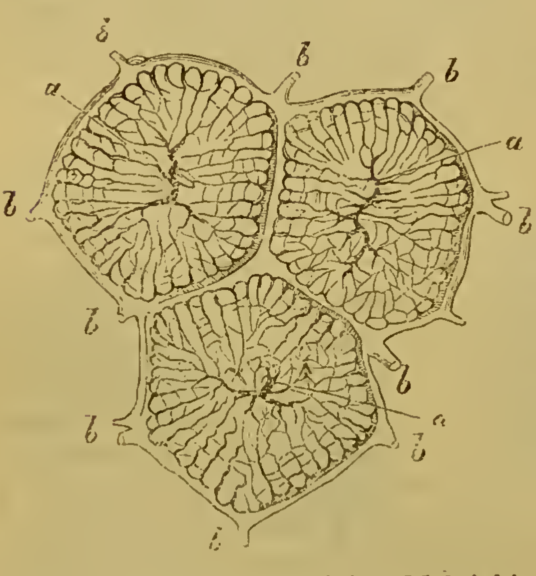


Fig. CCVIII. View of three lobules of the liver cut across, the centre of each occupied by the ramifications of the intralobular (the hepatic) vein, *a a a*. *b b b*, Branches of the vena portæ which course in the spaces between the lobules, surrounding these and constituting the intralobular veins. Numerous ramuscles penetrate into the interior of the lobules and anastomose with the intralobular or hepatic veins. The rounded and oval interspaces or islets between these vessels are filled or possessed by the biliary vessels (Fig. CCVII.) and form the acini of Malpighi. After Kiernan

creting element of the liver of mammals as hollow acini or vesicles with thin parietes, from the 40th to the 50th of a line in diameter, and capable of being distended by air thrown into the gall-ducts with which they are connected. For this structure we have the assurance of analogy, from what we witness in the constitution of the other glands, the mode of evolution of the liver itself, and the structure of the organ in the invertebrate series of animals. In fact, if we turn to the cray-fish and common garden snail, we find the precise structure in question. In the cray-fish the liver consists entirely of small pointed cœca clustered like grapes; in the snail it is made up of blind, rounded, terminal vesicles, which may be blown up with air from the biliary ducts[367]. If we farther examine the liver of the larva of the water-newt (Fig. CCIX. B.) we see distinct clusters of cœcal canals, or round terminal cells, like islets surrounded by subdivisions of the hepatic vein. But these cœcal canals at all events are not thin-walled cells; they are almost as compact as the acini of the fully formed liver of the highest mammal.

Elementary parts of Glands.

§ 196. The proper substance of glands is not formed by or out of the ordinary cellular substance, but by and from other more or less distinctly cellular elements. This anatomical truth is particularly evident in the liver (Fig. CCIV. A). Here the parietes of the acini consist entirely of compact, irregularly rounded or angular cells, of about $\frac{1}{200}$th of a line in magnitude[368]. The cells of the liver inclose

[367] See on this subject the representations of Müller in his work on the glands, Tab. viii., ix., x.

[368] The cells of the liver are particularly distinct. I have found the perfectly fresh human liver the most favourable subject for their demonstration. The blunt lobules of the liver (Fig. CCIV. A) appear to be entirely composed of them. Under pressure they immediately fall asunder into individual cells (Fig. CCIV. B). In the liver of a man of 40, who had shot himself, and whose body was examined in the greatest state of freshness possible, I found the very distinct rather angular than rounded cells not so very soft, but on the contrary capable of resisting a pretty considerable degree of pressure; they measured in the mean the $\frac{1}{100}$th of a line in diameter, but they were often of the $\frac{1}{80}$th and sometimes not more than the $\frac{1}{150}$th of a line in magnitude; they exhibited a distinct clear nucleus, which was rather smaller than a blood-corpuscle, and they were all filled with a fine molecular matter; several of them contained in addition larger deep-yellow or blackish molecules. [These dark molecules seem to be glo-

a distinct clear nucleus and a yellowish-coloured molecular matter in their interior. The cells are like the stones of a piece of ancient

bules of fatty matter, and the recent researches of Mr. Bowman (Abstract of paper read at the Royal Society, in *Lancet*, Jan. 22, 1842) have shown that the well known greasy or fat liver of phthisis is a consequence of its excessive accumulation—a very interesting fact in pathology, and doubtless connected with the imperfect oxygenation of the carbonaceous principle which must accompany respiration performed with a half or a quarter of the normal quantity of lung. R. W.]

Fig. CCIX.

A

B

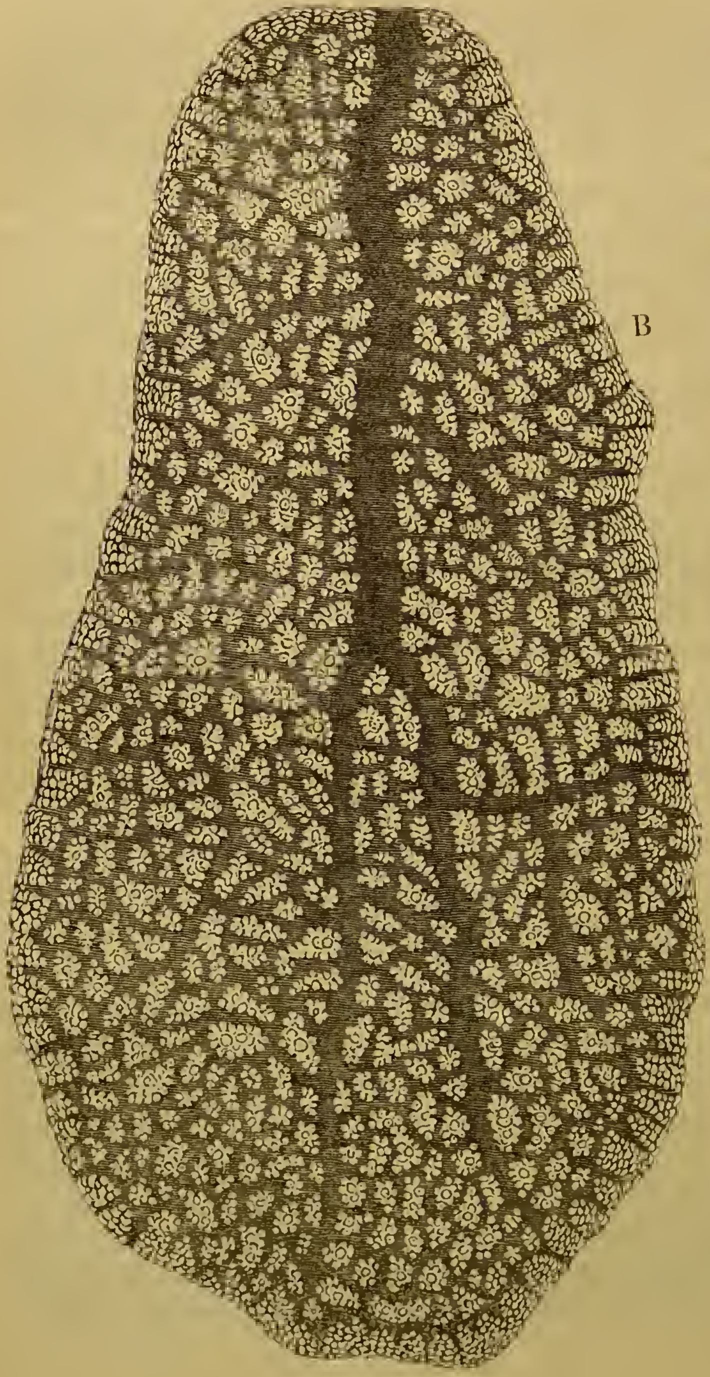


Fig. CCIX. A. A larva of the water-newt of the natural size; *a*, liver; *b*, stomach; *c*, gall-bladder.

B. The liver of this larva magnified 40 times. The dark coloured streamlets of blood are seen surrounding the hepatic lobules, which consist of aggregated racemiform cœca. The vascular channels represented are those of the hepatic vein.

masonry, irregularly applied to one another. Externally, where the blood-vessels play around them, fibres of cellular tissue are added. An epithelial covering of flat tessellated cells first makes its appearance in the larger branches and trunks of the gall-ducts. In other cases, as in the glands of the stomach, for instance (vide § 133), the substance of the glandular parietes consists of rounded dark granules, not obviously formed like cells, which appear to be arranged or packed between a very delicate external envelope turned towards the blood-vessels, and an internal epithelial investment[369]. The cellular structure of the parietes of the ventricular glands is however very apparent in young birds (Fig. CLXXIII. B). In other glands, moreover, we recognize the cellular structure with different degrees of distinctness,—in the tubuli uriniferi, for example, where the cells have nuclei, but are far from being so compact and are not nearly so readily isolated as in the liver (Fig. CC). It is difficult to say in how far this cellular structure, which may be followed to the very ends of the canaliculi, belongs to the innermost layer of the glandular paries, or is connected with the epithelial investment which appertains to the trunk and larger branches of the excretory duct of every gland. Apparently, however, there are always several layers of flattened cells placed one upon another, over which a structureless membrane is drawn externally, and this is the part that is surrounded immediately by the vascular reticulation. Certain it is, that wherever we find secreting follicles, they consist of a number of more or less distinctly cellular or fibrous layers, which lie as the proper substance of the gland betwixt the external net-work of blood-vessels and the inner wall whence the secreted matter distils away[370].

[369] I have already had occasion to mention the difficulty experienced in ascertaining the structure of the glands of the stomach in mammals. What relation the granules have to the substance of the gland has not yet been certainly ascertained.

[370] The minute structure of the glands is among the most difficult subjects of microscopical investigation, and we are still without a connected and complete treatise upon it, a want, however, that is likely to be soon supplied by Henle, whose observations will appear in the volume of the new edition of Soemmering's *Anatomy*, which he has undertaken to superintend. [The volume here alluded to has now been before the public for some months, and I believe that Mr. Smith will shortly make it accessible to the English reader in a translation. See farther on

Origin of the Glands.

§ 197. In our account of the DEVELOPMENT we have already had occasion to advert to this subject. We have seen that the greater number of the secreting glands arise from the mucous lamina of the germinal membrane, and like the salivary glands, the lungs, the liver, the pancreas, are to be regarded as evolutions of this membrane or of the intestinal canal. This view is liable to misapprehension, by the process of evolution being conceived in a purely mechanical way[371]. The general plan of the evolution of the secreting

the intimate structure of secreting glands in my account of Mr. Goodsir's views in the annotation under § 209, which treats of the mechanism of secretion. R. W.]

[371] All that has been lately urged against the admission of these laminæ of the germinal membrane, is quite just in so far as it is directed against a merely mechanical mode of viewing the structure. There is nevertheless a positive difference in the three layers of the germinal membrane, though no one has had this mechanical separation presented to him in nature in the same precise way as it has been used to convey a clear idea, a dogmatic exposition of the matter.

FIG. CCX.

Fig. CCX. Rudiments of the liver formed by evolution from the tractus intestinalis in the embryo of the fowl of the 4th day. After Müller—*De Gland. &c.*

FIG. CCXI.

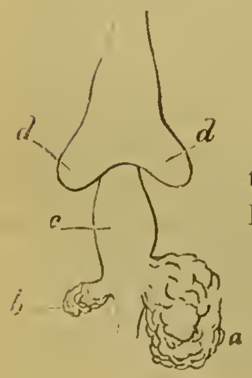


Fig. CCXI. Liver and pancreas of an embryo of the fowl at the end of the 4th day, magnified 12 times linear. *a*, the liver; *b*, the pancreas; *c*, the stomach; *d d*, the lungs.

glands is as follows. At the place where the gland is to be formed,—take the liver or the pancreas as a particular instance, (Fig. CCX. CCXI. & CCXII. *a b*), a rough projection appears upon the

FIG. CCXII.

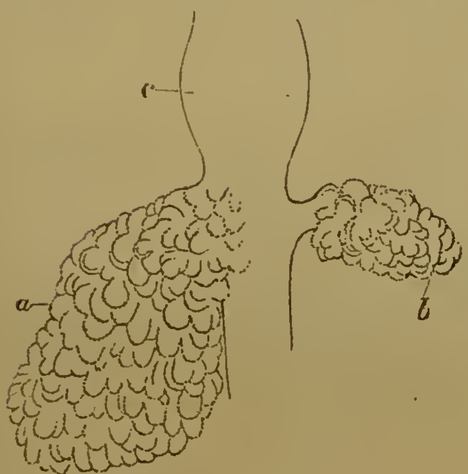


Fig. CCXII. The same parts in another embryo more highly magnified, to exhibit the undoubtedly cellular and racemose structure of the liver and pancreas.

FIG. CCXIII.

Fig. CCXIII. The liver more advanced than in last figure from an embryo of the fowl of the 6th day. It is not only divided into two lobes but shows minute cœca in its interior. After Müller.

FIG. CCXIV.

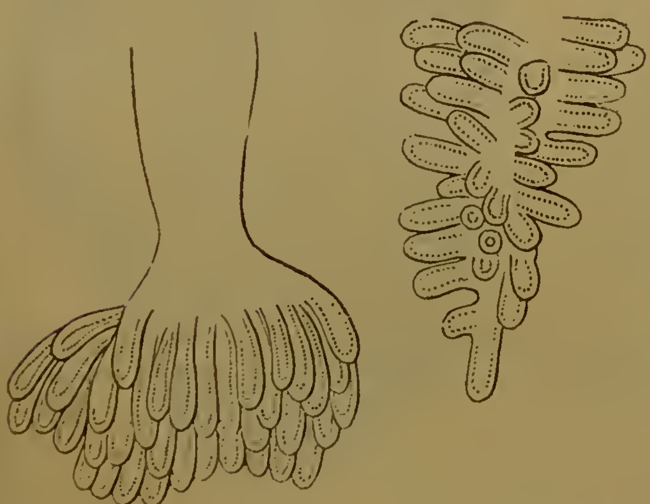


Fig. CCXIV. Ramifications of the bronchi from the embryonic Falco tinnunculus, to show the way in which they sprout as blind canals. Both figures are magnified about 150 times.

intestine. This projection consists of a delicate, finely granular, and pale tissue,—the *blastema,* as it is called, which was in former times looked upon as without structure. By watching this part we see how particular divisions make their appearance within it, (Fig. CCXIII.) which by and by form lobules or club-shaped bodies, and are the elements or ground-work of the future cœcal canals where these are to appear. It is now that a kind of solution of the internal contents of the mass or masses takes place, or rather that distinct walls with double contours are produced. This is to be seen most beautifully displayed in the lungs (Fig. CCXIV)[372]. And now appears the true glandular skeleton, as it has been described in speaking of the conformation of the glands. Would we follow this generation of the glands step by step, a gland must be chosen in which the ramifications of the excretory duct can be seen

[372] That the lungs are to be viewed as the prototype of all secreting glands has already been urged.

FIG. CCXV.

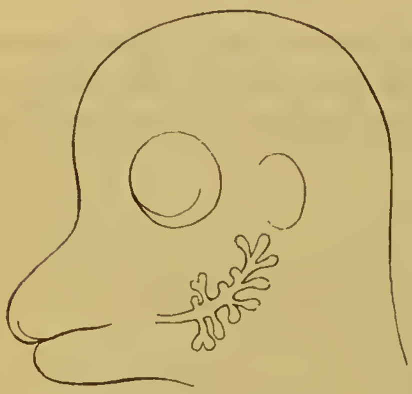


Fig. CCXV. Rudiments of the parotid gland in the embryo of a sheep, two inches in length magnified. After Müller.

FIG. CCXVI.

FIG. CCXVI. First appearance of the parotid gland in a human embryo of the seventh week; magnified twice.

amidst the clearer blastema, from the simple rudiment to the term of extreme complexity. In young embryos of the sheep (Fig. CCXV.) we can, with the aid of the simple lens, see the excretory duct of the parotid still simply branched, the several branches enlarged like buds at their extremities, and but seldom divided. The same thing may be seen in small human embryos (Fig. CCXVI.) To follow the onward evolution, embryos successively more and more advanced must be procured, and, the parotid being removed, it is to be examined with a low power and as an opaque object (Fig. CCXVII.) The clearer blastema of the gland now appears dark, and the excretory duct, which consists of a firmer granular mass, appears white and in the form of an elegant and numerously branched tree. The leaf-like ends now undergo transformation into blind vesicles, whilst the branches and twigs of the tree become hollow, and unite themselves to the excretory duct (Fig. CCXVII.) The blood-vessels are seen entering the blastema in the shape of dark ramifications (Fig. CCXVII.) but of much smaller diameters than those of the ramified glandular canal. The finest elements of the secreting follicles do not consist properly of cells; in the liver, for example (Fig. CCXVIII.),

FIG. CCXVII.

FIG. CCXVII. Lobules of the parotid gland with the excretory ducts from the embryo of a sheep four inches long, magnified 8 times. After Müller.

they are extremely soft, roundish, granular corpuscles[373], which give to the larger lobules (A) a racemiform appearance. It is betwixt these major divisions or lobules that the blood-vessels make their entrance (Fig. CCXVIII. B, *a*, *a*), none ever penetrating betwixt the finest elements of all[374].

373 When we speak, as we do here and in various other places, of *granules* in connexion with cells, it is meant to be intimated that there are formations to which the recent cellular theory has not yet been found applicable. One of the most distinguished among living physiologists, Purkinje of Breslaw, upon occasion of my notice of the work of Schwann (*Mikroskopische Untersuchungen, &c.*), the great importance of which was immediately and generally felt, observed with perfect propriety that it was still too soon to pretend to establish any general theory upon his observations, and that any such uniform formation of cells as undoubtedly occurred in the vegetable world, would not be very easy to indicate in the animal kingdom, that there were minute granular formations, elementary constituents of the animal tissues, &c., that could not with any show of reason or propriety be called cells.

374 The same formations are visible in 7 or 8 day embryos of the common fowl as well as in the embryo of the Falco tinnunculus; the liver is seen to be very distinctly composed of large granular but pale cells, which associate into imperfect racemes; a cluster of this kind (Fig. CCXVIII. A), measures $\frac{1}{50}$th of a line; between the clusters blood-vessels appear that seem to be without bounding parietes. The development of the glands of the stomach may also be very advantageously examined in such or in still smaller embryos. Here there are small thimble-like depressions observed, each of which represents a ventricular glandular sac, and consists of mere cells; every such depression is surrounded by a minute stream of

FIG. CCXVIII.

CCXVIII. A couple of feathery lobules from the embryo of the Falco tinnunculus or Hobby, 14 lines in length; the substance of the liver is seen composed of large pale granulated particles (cells); betwixt the lobules a blood-vessel is seen well filled with blood-discs.

Distribution of Vessels in Glands.

§ 198. Glands in general derive their blood from arteries, and all that is not used for purposes of secretion returns in the usual way through veins and lymphatics into the general current of the circulation. The lymphatics of glands are often very large and conspicuous; those of the liver are particularly so. Among vertebrate animals the liver receives but a small portion of its blood from an arterial source, and this appears to be exclusively expended upon the gall-bladder, the gall-ducts, and the coats of the larger vascular trunks, though branches of the hepatic artery can also be followed entering along with the cellular substance of the organ between its several component lobules. The blood from which the bile is prepared is received from the portal vein, which ramifies through the substance of the liver, and at length anastomoses with the finest subdivisions of the hepatic vein, which spring from the deeper parts and then flow round about the clusters of hepatic cells united into cœcal-looking lobules (Fig. CCIX. B). In the two lower classes of vertebrate animals there is an extension to the kidneys of the same system of circulation which we observe among the two higher classes confined to the liver. In amphibia and fishes a portion of the blood returning from the hind-legs, tail, abdominal parietes, and even some of the viscera, is distributed to the kidneys[375]. But whether the material for the secretion of the urine is

blood-corpuscles in the form of a wreath, which just occupies the space between one sac and another. On the development of the salivary glands vide particularly Müller loc. cit. and E. H. Weber in Meckel's *Archiv*, f. 1827, tab. iv.

[375] One of the most important and difficult tasks in organic chemistry, were to investigate the differences in the blood circulating through the interiors of different organs. Scarcely has a single step been taken towards solving this problem. Vide § 199 and Annot. 378. The blood which would obviously lend itself best to inquiries in this direction would be that of the portal system. C. H. Schultz (*Der Lebens-process des Pfortader-systems, &c.*, *The Vital Process in the Portal System*, &c. a paper read before the Hufelandian Med. and Chirurg. Society of Berlin, 1837,) says: "The peculiarities of the blood of the vena portæ appear to be intimately connected with the nature of the motion of the blood in this system, and its peculiar office. The blood of the portal system contains a smaller quantity of organized plasma than ordinary arterial and venous blood, whence the smaller quantity of fibrine obtained from it and the less perfect coagulation it undergoes; but in all its constituents there is a much larger proportion of a peculiar brown fat, and a great preponderance of colouring matter in the en-

afforded from this source or not is doubtful; for the kidneys here still receive arteries of considerable magnitude, the finer twigs of

velopes of the blood-corpuscles (the capsules of the blood-vesicles, *Auctor*), and proportionally less albumen also of peculiar quality. The whole blood is more watery, and coagulates imperfectly by reason of the less perfect constitution of the plasma, and sometimes it will not set at all. It were interesting to inquire into the origin of these peculiarities of the blood of the portal system, and farther into the purpose they serve, and the influence they exert on the motions of this blood." [Dr. Schultz's view of the portal system is very mysterious. He conceives it to stand in a particular relation with the blood-corpuscles, which here undergo a degeneretion : the capsular element of these bodies becoming excessively developed, the nuclear and more essential element, on the contrary, suffering absorption even to entire disappearance, loc. cit. p. 7. My friend Mr. Gulliver has examined the blood of the portal system again and again, and has never been able to perceive any marked difference between its corpuscles and those of the blood of any other vein of the body; and he has also found those organic germs which he has described and depicted in Gerber's *Anatomy*, in fibrinous clots obtained from the portal and splenic veins. For my own part, I see no mystery whatsoever in the portal circulation. I do not believe that the principles of bile are contained in the blood of the vessels which join in the formation of the vena portæ, in larger quantity than in the blood of the vena cava, any more than I imagine that the principles of urine are contained in larger quantity in the blood of the emulgent arteries than in that of the common iliacs. Bilin and urea—taking the two distinguishing principles of bile and urine as their representatives—seem to be alike products of the vital chemistry which goes on in every individual constituent atom of the body. We have evidence of the existence of bilin in the blood at all times, in the phenomena of bruises; and Magnus has shown that urea is always present in the circulating fluid. I view the portal circulation as a simple means of economizing arterial blood. The supply of so large a viscus as the liver with arterial blood, would have implied an increase in the pulmonary system especially, to an extent that must have been felt as inconvenient. Had the liver been furnished with arterial blood as the means of affording bile, it must obviously have had a vessel sent to it of a calibre equal to the sum of the vessels whose contents are finally collected into the portal vein. But Nature goes to work more economically; she first uses the blood of the great abdominal arteries to vitalize the viscera, and then, gathering this into a common trunk, she sends it to minister to the function of the liver; as a vivifying fluid this blood is exhausted, indeed, but subjected to the elective attraction of the liver it will still yield the elements of bile.

If we observe this husbandry of arterial blood in the higher animals, among which the respiratory system—the immediate agent in the production of bright blood—is most perfectly developed, we might, *a priori*, have expected an extension of the same economic plan in inferior grades of creation, where the pulmonic system degenerates so notably. And, accordingly, we see that in reptiles, where

which form such tangled knots as we observe in the same organs of birds and mammals. These tangled knots of vessels, Malpighian bodies as they are called, constitute a form of vascular distribution that is peculiar to the kidneys. They are skein-like convolutions of the arteries, which run in straight (Figs. CCXIX. CCXX.) lines between the tubuli uriniferi, before resolving themselves into the finest capillary net-works. They occur in largest numbers inter-

the lungs become cellular sacs, and among fishes, where they are replaced by gills, that not only is the liver, but the kidney also, supplied with venous blood, doubtless for the purpose of affording to each of these organs the materials of its appropriate secretion,—for to ask whether secretion can take place from venous blood or not? has always seemed to me a somewhat puerile question. Had not secretion been destined to take place from venous blood in man and the mammalia, Nature would not have been at the pains to distribute it through the liver in mammals and birds, through the liver and kidney in reptiles and fishes,—the existence of so peculiar an arrangement as we observe in the portal system of the liver and kidney, is already an answer to the question; the end of it is, as I have said, to economise arterial blood. Vide my paper on the Signification and Ends of the portal circulation in *Lond. and Edinb. Monthly Journal of Med. Science*, for Sept. 1841. R. W.]

Fig. CCXIX.

Fig. CCXIX. Malpighian bodies of the kidney of the water-newt (Triton palustris), after Huschke, in *Tied. u. Trevir. Zeitschrift*, B. 4, Tab. vi.

Fig. CCXX.

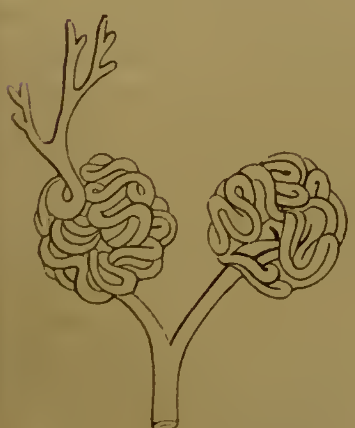


Fig. CCXX. Malpighian bodies from the kidney of an owl (Strix aluco), fully injected and largely magnified.

spersed among the tubuli uriniferi of the cortical substance, (Fig. CXCVIII. A and B.), but they are also observed more thinly scattered in the medullary substance.* The vessels of the most minute vascular net-works are everywhere much smaller—from twenty to thirty times smaller—than the finest cœcal and secreting glandular tubules, and never terminate in these, as they were once universally, and as they have even very recently been supposed to do.

* [Mr. Bowman, in a paper (*On the Structure and Use of the Malpighian Bodies*,) read before the Royal Society in February 1842, (Abstract in the *Lancet*, April 16, 1842) informs us that the results of his enquiries lead him to conclude that the Malpighian bodies consist essentially of " small masses of vessels contained within the dilated extremities of the uriniferous tubes." The tubes themselves consist of an outer transparent membrane lined by epithelium. This membrane is expanded over the knot or tuft of vessels, and constitutes the capsule described by Müller. The epithelium lining the uriniferous tube is altered in its character where the tube is continuous with the capsule, becoming more transparent and being furnished with cilia which act in a direction down the tube. The renal artery, after entering the kidney, divides into minute twigs—the afferent vessels of the Malpighian tufts. After the afferent vessel has pierced the capsule to which it belongs, it dilates, and suddenly divides and subdivides into minute branches, terminating in convoluted capillaries, which are collected in the form of a ball; and from the interior of the ball the solitary efferent vessel emerges, passing out of the capsule by the side of the afferent vessel. The ball lies loose and bare in the capsule, with which it is connected only by its associated afferent and efferent vessels. The efferent vessels, on leaving the Malpighian bodies, enter separately the plexuses of capillaries which surround the uriniferous tubes, and supply these plexuses with blood. The plexuses lie on the outside of the tubes, and from them the renal vein arises by numerous radicles. The blood in its course through the kidney consequently passes through two distinct systems of capillary vessels; 1. Through that within the capsules or extremities of the uriniferous tubes; 2. Through that on the exterior of these tubes. These efferent vessels of the Malpighian bodies Mr. Bowman describes collectively as constituting a *portal system* of the kidney, *i. e.* a system conveying blood between one capillary rete and another, like the vena portæ of the liver.—The anatomical facts here set forth are interesting and valuable, but it is probably a stretching of analogies to conceive the efferent vessels of the Malpighian bodies as elements of a portal system like that of the liver. The Malpighian bodies have been generally regarded as of the same essential nature as the retia mirabilia which we observe on the principal arteries of many of the lower animals; the efferent vessels of Mr. Bowman seem to me continuations of the renal artery, not veins. It would be difficult, too, it strikes me, to prove the origin of a uriniferous tube at each Malpighian body. The uriniferous tubes loop repeatedly, and pass round into one another—a fact which is against this idea. R. W.]

They rather play *round* the individual terminal portions of the glandular skeleton, they never even penetrate between the constituent cellular elements of this[376]. The parietes of the blood-

[376] The Dutch anatomist Ruysch is generally known to have made his minute injections a means of spreading abroad the error, at one time universally admitted as a truth, that the glands consisted entirely of blood-vessels, and so of throwing discredit upon the correcter notions of Malpighi, who admitted a peculiar glandular substance, although he was not acquainted with the finer elements of the glands. From the time that Haller advocated the views according to which the arteries were held to end immediately in the finest subdivisions of the excretory ducts of the glands, and not wholly and solely in veins, this hypothesis remained among the number of anatomical errors almost up to the present hour. Till Huschke, Weber and Müller appeared, it was held that an immediate transition of arteries into excretory canals must be admitted, more especially with reference to the kidneys. But since the great work of Müller upon the glands was given to the world, the prevailing analogical type in the relations of the glandular skeleton to the vascular system, appeared so obvious, and the conclusions come to obtained such general assent and confirmation, that the suspicions cast upon them by the school of Vienna, so celebrated of late years for its skill in minute injections, attracted the more attention, as the authority of this school has with justice been held great in this department of anatomy. Berres and Hyrtl have again described and represented, on the authority of numerous preparations, the immediate passage of arteries into the tubuli uriniferi. All that I have myself seen compels me still to give my undivided adherence to the views of Müller; even the dried and moist preparations of Berres and Hyrtl which I have examined, beautiful as I admit them to be, have not induced me to swerve in the slightest degree from this adhesion. I hold the doctrine of the anatomical distinctness of the capillary vessels and the secreting canals to be alone reconcilable with the fundamental principles of modern physiology. This abandoned, a host of indisputable facts of another kind must be abandoned also. I would not, however, be supposed to maintain that the frequent and perhaps even regular passage of fine injections from blood-vessels into secreting vessels observed by the Vienna school always depended on a laceration of the parietes of the containing channels. I believe it to be very possible that the very finest coloured molecules of an injection should penetrate between the component elements of the vascular and glandular structures, or perhaps even pass through them. [I remember to have heard Mr. Owen, in his Lectures at the Royal College of Surgeons, say that he could fill the tubuli uriniferi with an injection pushed from the arteries or not, at will. If he wished to fill the glandular tubes, he had only to use the finest vermilion of the shops, and to employ a certain amount of force with the syringe; if he wished to escape filling them, he had the fine vermilion of the shops carefully levigated anew, and then washed or elutriated, so that when a sample was examined under the microscope, no sharp angular particle appear-

vessels appear to be of the very thinnest and most delicate description in the glands[377].

Chemistry of Secretion.

§ 199. The constituents of the blood which is circulated through the capillary vascular system of the glands generally, must undergo a peculiar alteration. It seems indubitable that the organic substances held dissolved in the plasma,—the fibrin and albumen, afford the principal materials of the secretions; to what extent the hæmatin and the fat are made use of and altered in the glands is unknown. The proper cellular element of the glands seems to be the immediate theatre of the changes undergone. The way in which they occur, and the kind of chemical influence which the cells and tissue of glands exert are completely unknown, and can neither be explained from the nature of the elementary composition of the glandular tissue, nor from the relations of the mingled elements of the blood. It can only be owing to an extraordinary aptitude in the matters indicated to enter into new combinations, that changes in the proximate principles of the blood should by possibility take place in such short periods of time as they do within the glands. Organic chemistry, in spite of its boasted advances, leaves us here completely in the dark; yet from organic chemistry alone can we expect light upon the subject[378].

ed, and he was careful not to push his injection with any force. By these precautions he obtained as perfect an injection of the vascular tissues as ever, but completely escaped any penetration of the secreting tubules. R. W.]

377 It is not necessary to have recourse to injections in every instance to obtain the most perfect view of the distribution of the vessels of glandular parts. They may be seen in the greatest perfection upon the testis of our common small birds in the spring when these organs are in a state of peculiar turgescence.

378 [It strikes me that the above is purely speculative. We are without evidence that the fibrine, albumen, &c. of the blood undergo peculiar change in the secreting more than in any other organs. The only change they suffer is probably to the slight extent in which they must be altered to become constituents of the secreting organs themselves; they are not, for instance, turned in the liver and kidney into bile or urine any more than they are turned into carbonic acid in the lungs: the bile and urine and carbonic acid are in all likelihood engendered together in every constituent particle of the animal body during the interchange of elements which we know to be essential to vitality; and these substances are purged off from the general circulating fluid by appropriate

Chemical relations of the Secretion of the Urine, Sweat and Milk.

(BY DR. JULIUS VOGEL.)

§ 200. Healthy human urine is of a pale citrine or deeper reddish

organs; some of them are either engendered in such large quantity, or are so deleterious to the economy, that the whole mass of blood must be subjected to the purifying process in the organ specially connected with it—carbon or carbonic acid, for instance; others are produced so slowly, or are so little deleterious, that a part only of the blood is subjected to the action of the organ with which their elimination is connected; this is the case with reference to the bile and the urine. R. W.]

In the paragraphs that immediately follow, the chemistry of the secretion of the urine and sweat, the pure excreta of the system, is treated of in detail. The milk, too, must be viewed among those products of secretion which are of no service to the economy in which they are formed, and with reference to this, are therefore true excretions. The other secretions—the semen, saliva, bile, &c. have been considered along with the general apparatus of which they are the product and the vital processes in which they serve. We shall have occasion to speak of certain other secretions—that of the tears, for instance, by and by. The chemistry of secretion, in its connection with that of nutrition and with the vital processes at large, belongs to the general physiology.

This might be a fit place to say a few words on the present state of organic chemistry in its relations to physiology. One of the most distinguished chemists of the age has reproached physiologists with their indifference to the recent vast progress of organic chemistry, (see Liebig, *Organic Chemistry in its applications to Agriculture and Physiology*, Englished by Playfair. 8vo. Edinb. 1840) and has quoted passages from the writings of celebrated physiologists, the views embodied in which I am myself very far from sharing. I shall take at random a passage from a work in the first repute on organic chemistry—Berzelius's last edition (1840) 9th vol. p. 235, *by way of apology*. He says :—" I shall first give Braconnot's analytical researches on the liver as the most complete we possess. He took a portion by weight of the great lobe of an ox's liver, rubbed it down to a pulp in a marble mortar, diluted this with water, and strained it through a piece of fine taffeta. The greater part of the mass was found to have become dissolved, and passed through the filter, upon which the crushed vessels only were found to remain," &c. Such a procedure may be good in a chemical point of view, but when physiologically considered it is very objectionable. In this rude way, however, have all the analyses of organic parts which we possess been hitherto undertaken; the most varied and heterogeneous organic parts have been included in the analysis; what means, indeed, have we of separating the proper substance of the liver from cellular tissue, blood-vessels, blood, nerves, &c.? Has chemical analysis referred the manifold modifications of fibrine and albumen which con-

yellow colour, it has a specific gravity of from 1005 to 1030; a peculiar animal, sometimes a sweetish or aromatic odour, and a bitter saltish taste[379]. In general it shows weak acid reaction[380]. The tem-

stitute different tissues to any determinate laws? Do we know the constituents of the blood itself exactly? Can we upon chemical grounds explain the remarkable and most obvious difference in the colour between venous and arterial blood? These and many other questions are constantly propounded by physiologists to chemists, and answers to them are anxiously looked for. All, in congratulating each other on the progress of their respective sciences, chemists and physiologists, should now join hands and strive to make way in their researches together.

379 The colour of the urine presents every variety of shade, from the palest straw to the deepest orange or yellowish red; abnormal urine is still more diversified in its tint; sometimes it is turbid and chalky, which either depends on the presence of a precipitate of lithate of ammonia [or of phosphatic salts]; not unfrequently it is of a deep fiery red, but clear, and occasionally of a brownish blood-red, and turbid, the colour in the latter case depending on the presence of blood unaltered or decomposed; blue and black urine have even been observed. It is very proper to be aware that the normal urine will sometimes be deeply tinged of a red or blue with the colouring matter of cherries and other fruits. The specific gravity of the urine is also subject to great differences; it may exhibit any density between 1005 and 1030 without ceasing to be perfectly normal, the differences depending on the amount of water entering into the constitution of the urine. Any density above 1,030, almost certainly indicates something amiss. [I have lately examined the urine passed by two children, nearly of the same age, one of a slightly scrofulous constitution, the other very healthy, into a common vessel, and have been surprised to observe the high density which it sometimes possessed. The following are a few of the numbers:—November 29th, 1841, 8 A. M. 1031, 9 P. M. 1038; 30th, 8 A. M. 1034, 9 P. M. 1039; December 1st, 8 A. M. 1037, 9 P. M. 1037; 2nd, morning, 1027, night, 1035; 3rd, morning, 1029, night, 1035; 4th, morning, 1034, night, 1025. The children whose urine was the subject of observation are at this date (June 1842) in good health. R. W.]

380 The acid reaction of the urine depends on the presence of free lactic acid; an alkaline state of the urine is much rarer, but it does not always show anything morbid: the internal use of almost any of the neutral salts formed by the combination of a vegetable acid with a fixed alkaline base, and eating a quantity of those fruits that contain salts of this description, which all our subacid fruits do, will cause the urine to exhibit alkaline reaction. [A constantly neutral or alkaline state of the urine, without any cause of the nature of those just specified, is always a suspicious circumstance. It very certainly indicates something wrong with the digestive system, or a chronic affection of the uro-poetic system, which I should imagine apt to become serious. R. W.]

perature of the urine is that of the body, and varies from 96° to 100° F.

Urine just voided is generally clear; after it has stood for some little time, a very faint cloud appears in it, and slightly disturbs its transparency; this gradually subsides to the bottom, and when examined under the microscope, is found to consist of epithelial particles, mostly tessellated epithelial cells, derived from the urethra and bladder, connected by a little mucus, which in its original semifluid condition is scarcely perceptible under the microscope; it immediately becomes apparent, however, on the addition of a small quantity of alcohol or acetic acid, reagents that cause its coagulation, when it presents itself as an amorphous mass. Healthy urine rarely lets fall any proper deposit; the urine that is voided in diseased states of the system, on the contrary, very constantly does. The most common of all the sediments is that which consists of urate of ammonia; this is generally of a reddish yellow or pink colour, and disappears—being redissolved—when the urine is heated. A sediment of uric acid is also not uncommon; this, though amorphous in some cases at the first, soon shows itself as distinct crystals, having the form of rhomboidal tables, and being generally of a red colour. After the use of certain articles of food which contain oxalic acid, sorrel for example, [rhubarb and tomatas], the urine, normal in all other respects, always contains small shining octohedral crystals of oxalate of lime. The quantity of urine passed in 24 hours is very variable in the same individual at different times; it may not exceed a pound or a pound and a half, it may amount to as many as four or five pounds. In states of disease we have fifteen or twenty pounds of urine, and more, discharged in the course of the day[331].

[381] A friend of the writer during his tardy convalescence from a serious attack of disease, was at the pains to note the quantity of his urine, and also of the solid and liquid food which he took every day for a period of more than six months. The whole quantity of urine passed during 189 days, from the middle of November to the middle of May, amounted to 9817 loths, Bavarian measure [A loth is about half an ounce. R. W.] so that the mean quantity for a day appears to be 51,94 loths (very nearly 26 ounces). The largest quantity discharged in any day was in November, when 111 loths, or more than double the amount of the mean, were discharged; the smallest quantity discharged in any day was in April, when 29 loths, rather more than the half of the mean, were

§ 201. the chemical constituents of the urine are pretty accurately known, this fluid having been a favourite subject of analysis with chemists from the remotest times. They may be divided into essential constituents, or constituents which are always present in normal urine; and into accidental constituents, which are either substances used as food, medicine, &c. more or less altered, and passing off with the urine, or they are substances which are the product of a morbid secretion of the urine. The essential constituents of the urine, besides water, which always constitutes the great bulk of the fluid, are the following. *Urea*, a peculiar highly azotized organic substance which comports itself as a base to acids, and forms crystallizable salts with them. *Uric acid*, an animal acid peculiar to the urine, of the most sparing solubility in water. It is not yet perfectly ascertained by what substance it is held dissolved in the urine[382]. *Animal extractive*, similar to that which is encountered in the other fluids of the human body. *Lactic acid* and *lactates*, which are also met with in the greater number of the fluids. A *red colouring matter*, the chemical nature of which is not yet well known. A variety of *inorganic*

voided. In winter the quantity of urine passed is larger than in summer, a fact which appears from the observations just referred to; the daily average for November was 66 loths; that for December $57\frac{1}{2}$ loths; that for January 57 loths; for February $54\frac{1}{5}$ loths; for March $46\frac{1}{5}$ loths; for April $40\frac{2}{3}$ loths; for May $40\frac{1}{3}$ loths. In the summer months it would in all probability have fallen still lower. From the same observations we learn, farther, that in general the quantity of urine discharged stands in a certain ratio to that of the fluids imbibed; but that the quantity of urine does not regularly increase and diminish with the quantity of fluid consumed, as we might have expected that it would. Whilst on many days the urine scarcely amounted to a third part of the fluids (fluid aliments such as soup, &c. inclusive) consumed, on other days it equalled these in quantity, and on others it surpassed them by a 20th, and even by a 10th. The observations referred to apply only to an extremely regular and sober life. Drinks taken in excess invariably induce, and that generally in a very short space of time, an increased flow of urine.

382 Urea and uric acid are the proper characteristic ingredients of the urine; the uric acid has been perhaps more carefully studied in the excellent researches of Liebig (in *Annalen der Pharmacie*, Bd. 26. S. 241) than any other animal substance. Urea, as Wöhler first showed, may be produced artificially, and is a compound of cyanic acid, ammonia and water, a cyanate of ammonia with combined water. The purpuric acid of Prout, which has so commonly been regarded as the colouring principle of the ruddy sediments of the urine, is still problematical.

salts—sal-ammoniac, common salt, phosphate of soda, phosphate of lime, sulphate of lime, magnesian salts, and a trace of scilica[383].

§ 202. Besides the essential constituents of the urine already mentioned, it often contains accidentally admixed matters in large quantity. Many articles of food, of drink, and of medicine, pass unchanged or changed into the urine. The greater number of the inorganic neutral salts make their appearance in it unaltered: among the number may be reckoned the sulphates, phosphates, and nitrates of potash, soda, and magnesia, the chlorides of potash, soda, and ammonia, the various iodides, the greater number of the tartrates (?); a variety of organic substances, the major number of the vegetable colouring matters, as of rhubarb, bilberries, cherries, beetroot, madder, indigo, &c.; various animal and vegetable odorous principles, such as turpentine, valerian, castoreum, &c. Free acids taken into the stomach generally make their appearance in the urine in combination with bases, the oxalic acid generally as oxalate of lime [the benzoic acid in combination with uric acid as urobenzoic or hippuric acid,] iodine and bromine, which play the part of acids, as iodides and bromides. A great many of the organic acid salts, as the citrates, malates, and acetates, appear as carbonates[384]. Many substances, such as lead, alcohol, ether, musk; and certain colouring matters, such as litmus, cochineal, &c. have not been discovered in the urine though taken into the stomach[385].

383 The urine in children has been found to contain hippuric or urobenzoic acid instead of uric acid. [The very interesting fact has lately been announced by Mr. Ure, that it is easy at all times to supersede the presence of uric acid and the urates in the urine, by administering the benzoic acid or an alkaline benzoate by the mouth, either of which, after being absorbed into the blood, passes off by the kidney, and combining in its transit with the uric acid and the urates, forms hippuric acid and hippurates, which, as compounds that are readily soluble, escape with the urine. The advantages which may accrue from our knowledge of these facts in the treatment of certain calculous diatheses, and perhaps even of gravel and stone of certain kinds existing in the kidneys and bladder, are obvious, R. W.] Berzelius once found butyric acid in the urine, and other chemists are said to have detected acetic acid and acetates there; but it is very doubtful that any of these articles are components of the normal urine.

384 This alteration of the generality of the organic acid salts into carbonates appears to go on in the stomach during the process of digestion. See § 156.

[385 Von Bibra (*Unters. uber einige verschiedene Eiterarten*, 8vo. Berl. 1842,) has found that sugar, taken in large quantity after long fasting, could be demonstrated both in the blood and in the urine—a very interesting fact. R. W.]

§ 203. The best quantitative analysis of the urine we yet possess is that of Berzelius, who in 1000 parts of that which he examined found :—

Water	933,00
Urea	30,10
Free lactic acid, lactate of ammonia, osmazome, extractive matter only soluble in water	17,14
Uric acid	1,00
Mucus	0,32
Sulphate of potash	3,71
Sulphate of soda	3,16
Phosphate of soda	2,94
Biphosphate of ammonia	1,65
Common salt	4,45
Sal ammoniac	1,50
Phosphate of lime and magnesia	1,00
Scilica	0,03
	1000,00

The quantitative relations here given are to be understood as but one of millions that are possible. The composition of the urine in different individuals is habitually very different, and even in the same individual it differs greatly at different times. An attempt has been made to reduce these varieties to certain general laws: 1. The watery portion of the urine is by so much the larger as the quantity of simple drink is large; the water is farther in larger proportion in winter than in the summer and when the cutaneous perspiration is freer. The quantity of the urine, in the healthy state at all events, depends especially on the quantity of its water; the larger the quantity of urine discharged, the greater in a general way is its watery part[386]. 2. The quantity of urea and also of uric

[386] I have made quantitative analyses of a great number of specimens of urine of different individuals in health and labouring under disease, and have come to the following conclusions in regard to the proportions of water and of solids. The minimum of solids in 1000 parts of urine was 12,5; the maximum 71,5. The quantity of water consequently varies between 987,5 and 928,5. As a mean of 40 analyses, I obtained 40,0 in the 1000 of solids, the mean of the watery part was consequently 960,0. The urine examined was generally that which was discharged in the morning.

acid discharged by the same individual in equal intervals of time are, in a general way, equally great; but in different individuals they may be very different[387]. 3. The quantity of urea voided in a given interval of time is in relation with the sex and age of individuals: it is larger among men than women, and among persons of middle age than children and the aged. 4. The quantity of the inorganic constituents—salts—of the urine, is never the same in the same individual in like spaces of time; the urine of men however generally con-

[387] This and the following laws from 2 to 4 are given on the authority of Lecanu (*Comptes Rendus*, 1839, ii. Semest. p. 84). Dr. Fr. Simon has also examined the urine of numerous individuals with regard to the quantity of urea they contained (*Archiv d. Pharmacie, von Brandes, &c.* Aprilheft, 1840, S. 37). He found as a minimum in 1000 parts of urine 3,16 urea, (6,0 nitrate of urea); as a maximum 24,69 (47,5 nit. of urea). In one case the entire quantity of urine discharged in the course of 24 hours amounted to 15 pounds, apothecaries weight, which in 1000 parts contained 3,16 of urea, in the whole consequently 4,55 drachms of urea. I have also examined the urine of many persons with reference to the quantity of urea especially which it contained, and found as a minimum in 1000 parts 2,5; as a maximum 29,8 urea,—greater differences consequently, than Dr. Simon observed. But such estimates of the quantities of urea only admit of conclusions in regard to the normal or abnormal constitution of the urine when the whole quantity passed during a certain period—24 hours, for instance, is collected and subjected to analysis. But such collections of urine are at all times inconvenient, and occasionally impossible to be made. I therefore subsequently estimated the relations of the urea to the entire quantity of solid constituents which the urine contained, a plan by which more invariable results are obtained. The following results were come to in this way: in 1000 parts of the solid constituents of the urine the maximum of urea was 55,4, the minimum, 13,0; mean of these extremes, 34,2. Mean quantity of urea from 17 analyses 35,4. I obtained the urea in the same way as Simon, viz.: in the state of nitrate, estimating the absolute quantity of the base from the known constitution of this salt. Neither of the two methods of proceeding, however, gives any absolutely precise result.

The quantity of uric acid in the urine is but small, and there are particular difficulties in the way of estimating its relative proportions. The quantity of this substance contained in the urine of healthy individuals, if I may be allowed to conclude from a small number of analyses, appears to be subject to fluctuations of no great amount. The medium proportion of uric acid in healthy urine is not far wide of that in the analysis of Berzelius given above, viz: 1 in 1000 parts of the fluid. But the quantity of the substance in question is enormously increased in many diseases, in rheumatic fever and gout, for instance.

tains a relatively larger proportion of salt and salts than that of women[388].

Sweat.

§ 204. Under ordinary circumstances the sweat is so gradually poured out that it does not appear as a fluid at the orifices of the sweat canals, but passes off in the shape of a vapour as fast as it is secreted, leaving behind it however its fixed or unvolatile ingredients. It is only under exposure to high temperatures, along with active bodily exertion, in the course of various diseases, under the influence of medicine, &c., that the sweat is elaborated in such quantity as to stand in drops upon the skin, and to be collected for examination. The sweat in the liquid state is a clear and colourless fluid[389], of a sourish or ammoniacal odour, and slight saline taste. In a general way the sweat shows alkaline reaction; at other times it does not affect vegetable blue colours; but the sweat of many parts of the body, the arm-pits, for instance, is said always to react like an alkali[390]. The sweat has no peculiar solid element, [its

[388] Leeanu tells us that he always found a larger quantity of common kitchen salt in the urine of men than of women. On the fixed saline constituents of urine, —I mean the saline eonstituents that withstand incineration and the action of nitric aeid,—I have made many researches, and ean vouch that they are subject to great variations. In 100 parts of solid urinous residue, I found a minimum of 7,7 and a maximum of 73,5 of fixed saline matters. The mean of 21 analyses was 28,2. This average, however, is certainly too high, for many of the individuals whose urine was analysed were ill and taking neutral salts; the patient, for instance, whose urine afforded the largc proportion of 73,5 per cent of fixed saline matter was taking acetate of potash, and ¾ths of the salts obtained were salts of potash. I have repeatedly observed that the salinc matters of the urine increased when patients had neutral salts prescribed to them. [Probably the most useful of all the analyses of the urine for the praetitioner is that which determines the relative proportions, 1st. of the solid ingredients to the mass; 2nd. of the solids soluble in alcohol only (Laetie acid, lactates), 3rd. of the solids soluble in distilled water, (sulphates, ehlorides and carbonates), 4th. of the solids insoluble in aleohol and in water (phosphate of lime, of magnesia and ammonia, and uric acid). One of the most important of all the abnormal eonstituents of urine is albumen; but this subject is within the domain of pathology, not of physiology.

[389] The sweat is very seldom eoloured; it is so, however, oeeasionally, in icterus perhaps most frequently, whcn it is yellow and stains the linen of this eolour; bluc, and red or bloody swcats are also said to havc becn observed.

[390] Donné in his lectures says the sweat of the axillæ is always alkaline, that

salts and other constituents exist in all the fluids of the body and in the blood itself]. After evaporation upon a clean glass plate, fragments of epidermic cells are generally observed in the sweat, and crystals are left behind which are those of its contained salts.

Chemical Analysis of the Sweat.

§ 205. The chemical composition of the sweat is not in all probability the same at all times. Its principal ingredient in point of quantity, is water, which generally forms something like $\frac{99}{100}$ths of its whole mass. It also contains animal extractive or osmazome in small proportion, and a variety of salts, the most abundant and constant of which are common kitchen salt, sal ammoniac, and certain lactates, which must sometimes be in the state of super salts, for an acid reaction of the sweat would seem to depend on lactic acid. Sweat farther contains minute quantities of phosphates and sulphates, and perhaps also acetic acid[391]. The sweat has also been found to contain certain gases—carbonic acid in especial, and a little azote[392].

of other parts of the body generally acid. I have generally found the sweat of the forehead, breast, and hands, without effect upon vegetable blues, and consequently to be neutral.

391 A drop of sweat evaporated on a glass plate leaves a residue which under the microscope, besides fragments of epidermis, leaves crystals of two descriptions, the one cubes—common salt,—the other clustered dendritic forms—sal-ammoniac. In 100 parts of sweat Anselmino found from ½ to 1¼ per cent of solid residue, which in 100 parts consisted, 1st, of substances insoluble in alcohol and water (calcareous salts, and fragments of epidermis) 2; substances soluble in water not in alcohol (animal extractive and sulphates) 21; substances soluble in dilute alcohol (common salt and osmazome) 48; substances soluble in anhydrous alcohol (osmazome, lactates and lactic acid) 29. Sal-ammoniac is not noticed in this analysis.

392 Collard de Martigny and many other inquirers before him, Cruickshank, Jurine, Abernethy, &c. showed that carbonic acid and azotic gas were thrown off by the skin; Anselmino also detected free carbonic acid in the sweat. [The purpose of the cutaneous exhalation has been avowed by all the highest authorities of the age in physiology not to be understood. The chemical analysis of the sweat is owned by Berzelius (*Chimie* vii. 330) to throw no light on the subject. "Water," he says, "is, in fact, the principal article thrown off by the skin." I believe it to be the only essential one, and reserving the development of the point for another opportunity, I merely state it here as a general thesis, that *the business*

Milk.

§ 206. As obtained from the breast of the human female by suction or pressure, milk is a somewhat thickish fluid of a bluish-white colour, without peculiar smell, and of the known milky flavour. Its specific gravity varies between 1028 and 1034. Quite fresh it generally shows alkaline reaction ; it is only after it has stood for some time—longer or shorter according to the temperature of the air—and when it is abnormal, that it shows acid reaction. Under the microscope it is found to contain an immense quantity of perfectly spherical globules of various sizes, from the $\frac{1}{200}$th to the $\frac{1}{600}$th of a Paris line in diameter, and having a great refractive power[393]. These globules are seen at the first glance to consist of oil or fat, and chemical reagents prove them to be so. They are in fact the butter, which is not dissolved, but only suspended in a state of minute subdivision in the milk. The oil-globules, according to some observers, are included in cysts of coagulated casein[394]. Milk may be freed from its oily or buttery part by repeated and careful filtering ; the same thing is habitually accomplished by whipping or churning, an operation which leads the divided buttery particles to unite and form masses.

According to Donné, the *colostrum* or milk that is secreted during

of the skin is to eliminate so much pure water, and this not to reduce or regulate temperature, as is eommonly said, but *for the specific end of maintaining the current of blood returning to the heart of higher density than that which is leaving it.* The skin is one item in a great system subordinate to the eapillary circulation, and its funetion is indispensable to the due return into the veins of the fluids exuded from the arteries for purposes of nutrition and vital endowment. Vide my addition to Annotation 342 ; and farther what is added under the head of NUTRITION, sect. 218—23. R. W.]

393 The most important works of recent date on milk are those of Donné : *Du Lait, et en particulier du celle des Nourrices*, Paris, 1837, and of Dr. F. Simon : *Die Frauen-Milch*, Berlin, 1838 ; the former treating more especially of the physical and mieroscopical, the latter of the chemieal properties of the fluid. We have also an interesting paper by J. E. Herberger, on the milk of women and the lower animals, in Brande and Wackenroder's *Archiv der Pharmacie*, Jan. u. Feb. Heft. 1840.

394 Henle and F. Simon (*Elements of Organic Chemistry*, *Animals*, p. 75. Berl. 1840) are of this opinion ; for my own part, I have never been able to satisfy myself completely of the existence of such an envelope.

the few first days after the birth of the infant, contains in addition numerous and somewhat larger corpuscles of irregular form and granular appearance, and which the observer quoted calls *granular bodies*. These bodies dissolve, like the ordinary oil-globules, in ether, and are probably the same as these in point of chemical composition. As the colostrum passes into or gives place to ordinary milk, these bodies disappear gradually, and finally cease to be visible[395].

Chemical Composition of Milk.

§ 207. The essential constituents of milk, besides water, are FAT (butter), CASEIN and SUGAR OF MILK[396]. In addition to these essential constituents, milk farther contains extractive matter[397], va-

395 Simon denies the existence of these granular corpuscles in colostrum; but Donné has shown them to me, and many others, in the course of his lectures, so that there can be no doubt of their existence. The following questions, however, still remain to be answered:—Are they always present in the colostrum, what is their import, and what do they consist of? Are they perchance mere irregular masses of fatty substance, or deposits of a matter peculiar to the colostrum and not contained in the milk? Farther inquiry must determine these different questions.

[The great rapidity with which glandular secretion takes place under the influence of the appropriate stimulus, is perhaps in no instance more strikingly illustrated than in reference to the milk. When the infant is applied to the breast, the mother feels a sudden rush to her bosom, and almost immediately it becomes distended with milk, which pours from the orifices of the ducts. This rush is popularly termed the *draught*, and mothers think it is caused by the milk filling the breast; the scientific explanation of the sensation is the sudden injection of the arteries of the secreting organ with blood. But the popular explanation is not altogether erroneous; the injection of the arteries and the distension of the milk ducts are almost simultaneous, and the rapid filling of these last has probably still more to do with the peculiar sensation experienced than the propulsion of the blood with unusual rapidity and in unwonted quantity through the vessels of the secreting organ. R. W.]

396 All the constituents of the milk, with the exception of the fat and perhaps a minute quantity of casein, are in a state of solution in the milk. The butter of human milk consists, according to Herberger, entirely of elaine and stearine, without any of the peculiar fatty matter which has been called *butyrin*, and which the butter from cow's milk contains.

397 The alcoholic extractive matter of milk, according to Berzelius, is precisely similar to that of muscular flesh; milk seems to contain but very little watery extractive.

rious salts, and very commonly some free lactic acid, which, however, in all probability, only makes its appearance when the milk begins to turn. The following analysis of Dr. F. Simon will give an idea of the quantitative relations of these several ingredients to one another[398].

100 parts of woman's milk contain—

88,06	water
3,70	casein
4,54	sugar
3,40	butter
0,30	salts, extractive matter, &c.[399]

§ 208. The quantities of the several constituents of the milk are not always the same; they are indeed subject to vary greatly, so that milk is rich or poor, more or less nutritious. Simon was at the pains to search after the laws that regulated these differences in the relative proportions of the several ingredients of milk, and came to the following conclusions: The colostrum or milk that is secreted the first few days after delivery is richest in solid constituents; the few first days past, the quantity of casein is very small, but it increases subsequently and then continues very constantly the same. The quantity of sugar, on the contrary, is greatest immediately after the delivery, and then diminishes somewhat as the casein increases. The proportion of fat or butter is subject to the greatest variations, which cannot be reduced to any law[400].

398 This analysis may be adopted as indicating with tolerable accuracy the composition of normal human milk containing a medium quantity of nutritive matter.

399 The salts of milk are principally chloride of potassium, lactate of soda, and phosphate of lime. Some chemists speak of certain sulphates as entering into the composition of milk, but these, as well as a portion of the phosphates, are produced by the incineration of the milk, the sulphur and phosphorus which are in combination with the casein being turned into sulphuric and phosphoric acids.

400 Simon analysed 17 samples of milk, mostly obtained from the same female on different days, and found the following variations in the proportions of the several essential ingredients. The maximum of casein found in 100 parts of milk was 4,52, the minimum 1,96; mean of 17 observations 3,03. The maximum quantity of sugar found was 7,00 (in colostrum), the minimum 3,60; mean of 17 observations 4,83. The maximum quantity of butter was 5,40, the minimum 0,80; mean of 17 analyses 2,77. 100 parts of colostrum he found to consist of

A plentiful supply of nutritious food increases the quantity of milk in general, and of its buttery element in especial, without seeming to exert any particular influence on the proportions of sugar and casein. Diseases, too, affect the constitution of the milk; but a sufficient number of chemical researches in regard to the kind of alteration suffered are still wanting to admit of any general conclusions being drawn in regard to the influence of particular diseases upon the elaboration of the milk[401]. Many articles taken as food or as medicine are known to pass over into the milk,—the colouring matter of rubia tinctorum, the odorous principle of garlic, onions, turpentine, &c.; several neutral salts, too, make their way from the stomach into the milk; but all do not pass indifferently by this route; the ferro-cyanate of potash, for instance, though it is readily to be detected in the urine, can never be shown to occur in the milk[402].

Organic Phenomena of Secretion.

§ 209. The secretions are eliminated from the blood, and the processes that give rise to them have their seat in the substance intermediate to the walls of the finest blood-vessels and the inner aspect

82,80 water, 4,00 casein, 7,00 sugar, 5,00 butter. Donné proceeded on the assumption that the quantity of sugar and of casein in milk was always in relation with that of the butter, and therefore proposed microscopical examination as a ready means of testing the quality of a nurse's milk, the quantity of butter-globules in the milk being to be estimated approximatively with tolerable accuracy. The experiments of Simon just quoted have shown that this idea of Donné is unfounded, and that his mode of testing the nutritive qualities of milk must be rejected.

401 Both Simon and Herberger have given several analyses of diseased or morbidly altered milk. [Gerber has given an excellent delineation of the globules of healthy cow's milk; as well as of slimy, imperfectly coagulated, and reddish-coloured milk, from a cow which had died of the poll-evil, in which diseased milk the globules are shown as connected together by a thick fluid. *General Anatomy*, figs. 22 and 23. R. W.]

402 Simon could not discover iodide of potassium in the milk, although the readiness with which it passes by the urine is known. Others have been more fortunate than Simon, Herberger for instance, and have detected this salt in the milk as well as in the urine. We are still very much in the dark in regard to the laws that regulate the transit of different substances taken into the stomach into the various secretions and excretions.

of the glandular tubules, vesicles, or follicles. All that we learn from the study of the minute anatomy of the glands, as detailed in sundry preceding paragraphs, indicates that the alterations in the combined elements of the blood which give rise to the secretions go on in that portion of the plasma which has penetrated the glandular substance; part of this is appropriated as nourishment, part is turned into the specific secretion. Of the way in which this happens we know nothing; we have no data for reasoning, and are therefore reduced to mere hypothesis; neither minute anatomy nor organic chemistry come to our assistance here. The glandular skeleton of each particular secreting organ presents immense variety in different classes, and even in different members of the same class, of animals (vide § 188 which treats of the salivary glands of insects, and in which the testis of the same extensive class is spoken of), without the secretion therefore exhibiting any striking or essential differences[403]. The proper substance of glands in general, indeed, histologically and chemically considered, exhibits no great diversity[404]. The vascular net-works, too, are coordinated with the structure and connections of the individual parts of the glandular skeleton, and neither present specific forms, nor give any clue to the specific qualities of the secretion[405]. The specific in the secretions

403 In general, indeed, particular glands exhibit a particular and determinate arrangement of their elements—the kidneys, for example, always present a tubular, the liver for the most part a granular or acinous structure, and so on. The liver, however, it must be allowed, exhibits great diversities of form among the members of the invertebrate series,—in the crab, to select a single instance, where the bile has nevertheless the same colour, constitution, &c. as in the vertebrata. The structure of those glands, moreover, whose secretion is the most truly specific of any—the testis,—is extremely different. Even among the vertebrata, where the general structural type is so closely preserved, we perceive great differences in the testis of different classes,—what can be more dissimilar than the structure of this gland in the mammal and in the fish, for example? and on the contrary, organs of very dissimilar function often present great similarity in point of strucure—the testis and the kidneys, to quote a single instance.

404 More careful inquiry might perhaps lead to the detection of exceptions here, and so to important discoveries. We find that glands, the secretions of which are of very dissimilar and decided character, also exhibit histological differences or peculiarly organized elementary parts;—the gastric glands with their granules, the liver with its compact cells, may serve as examples of this fact.

405 These relations have already been the subject of remark (§ 198); it is

however is, after all, not more wonderful than the specific metamorphoses of the constituents of the blood into the elementary constituents of the various tissues, in the process of their nutrition. Wherein the essence or special ground of the vital or organic agency mutually exerted between the constituents of the blood and the glandular tissues, consists, transcends our science to unravel. We assume, however, 1st, That the glandular particles select from the blood by a kind of elective affinity those matters which are necessary to the composition of their secretions; 2nd, That the alteration of matters takes place either by a chemical action within the cells, or,—and this is less likely,—that it is effected by a liquefaction of this cellular substance itself[406]. It is obvious, however, that even in

worthy of observation, nevertheless, that in reference to particular glands there are constantly recurring peculiar modes of distribution of the blood-vessels. The liver, for example, receives blood from a particular and appropriate system, that, viz., of the portal vein; and the arteries of the kidney exhibit almost invariably those peculiar convoluted knots which are known under the name of the Malpighian bodies. But we must still bear in mind that in the invertebrata the liver secretes bile, and certain glands which are comparable to the kidneys, separate uric acid without the organs having blood supplied to them from a particular source, or distributed in any particular manner to work upon. [The kidneys among the higher animals, more than any other secreting organ perhaps, receive the blood directly from the great arterial stem of the body. The renal arteries are large and short, and the column of blood they contain must therefore be exposed to the full force of the heart's impulse. The Creator has probably had recourse to the tortuous coils called Malpighian bodies to break the force of the current, and to prevent the blood in the capillaries from being pushed too rapidly through them, and only partially exposed to the peculiar elective powers of the proper substance of the organ. Far from the heart being inadequate to suffice for the circulation of the blood in every part of the round, as it has often been held, we here see impediments thrown in the way of a too ready passage from the efferent to the afferent order of vessels. The source whence the blood is derived that is subjected to the elective affinities of the glandular organs of excretion is, I apprehend, of no moment. Vide my Paper on the Signification and Ends of the Portal Circulation in *Lond and Edinb. Month. Med. Jour*. Sept. 1841. R. W.]

406 [One of the most important contributions lately made to the physiology of secretion is that of Mr. Goodsir (Paper read before the Royal Society of Edinburgh, March, 1842, abstract in *Annals, and Mag. of Nat. Hist.* May, 1842) who has carried out this idea, and maintains that the constituent cells of glands are the ultimate secreting structures, and that growth and secretion in glandular organs are identical. It is familiarly known that the peculiar secretion of many glands is found within their component nucleated cells, for instance, the *ink* in

demonstrating the one or the other of these views, nothing essential would be gained, that the grand and final question would in fact only be put off. An important step in advance would be made, could we obtain any data for answering the questions connected with the specific nature of the secretion in each particular gland; for each gland only separates the secretion which it was originally destined to prepare. The entire subject rests on the fact, that certain constituents of the blood are eliminated in large quantities under certain circumstances at certain places, these ingredients only presenting themselves in very moderate quantity elsewhere; or, in other cases, and where there is a large quantity of blood present, along with the ordinary constituents of a secretion we have extraordinary matters separated from the blood. And this last only applies to the depürative secretions, or proper excretions.

the appropriate gland of the cuttle-fish, the purple in the peculiar gland of Ianthiaca and Aplysia, bile in the cells of the liver of animals in general, urine in those of the kidney of molluscs, &c. *The history of secretion*, in fact, as Mr. Goodsir shows, comes to be *a history of the origin, evolution and disappearance of the nucleated cells which make up the substance of glands.* These cells in different glands are evolved singly, or several of them are evolved inclosed in a common capsule. In either case they gradually attain maturity, and are more and more replete with the secretion of the organ of which they are elements. Perfectly mature, they are found connected with the side or extremity of one of the terminal ducts, but separated from its canal by a fine diaphragm, part of the primary cell-wall. This at length gives way, the matter included in the cell or group of cells is shed into the duct, and this cell or group of cells disappears, its place being immediately succeeded by another which will undergo the same changes. This ingenious view, which is akin to that originally broached by Purkinje, explains satisfactorily wherefore a secretion flows from the free surface only of a secreting membrane,—the cells which contain the secretion are there only in a state of maturity, and there incessantly giving way and pouring it out; just as the cells of the cuticle or epidermis are continually detached from the free surface, being pushed off by those that are evolved behind them. I would beg to suggest a farther extension of the same grand view to nutrition in general; what becomes of the cells which constitute the muscles, and all the other tissues of the body? they must needs be in a state of perpetual decay and renovation. Let us look at the absorbent system of vessels as the essential element of an universally distributed gland, and the question I have asked is easily answered: the constituent cells of all the animal tissues as they decay burst into an absorbent canal and so are removed, or the fluid into which they finally resolve themselves finds its way into an absorbent and so is removed. R. W.]

§ 210. The whole of the secretions stand in a determinate equipoise partly to one another, partly to nutrition. With reference to the depurative secretions that take place in the lungs, in the kidneys, and in the skin, such an equipoise is more especially remarkable, and is constantly indicated under the title of the antagonism of the secretions[407].

As every secretion is instituted with reference to the abstraction of certain ingredients from the blood, and as the constitution of the blood is necessarily altered by the retention of the elements of this or of that secretion; farther, as every secretion has its specific destination, every disturbance of a secretion, whether in a qualitative or quantitative point of view, must induce disturbance in the whole organism, and this may be manifested, in the vicarious activity of an antagonist secretion[408]. If this be not possible, then disturbances in the nutrition follow, and these lead to or constitute diseases. It must be presumed in general, that according to the constitution of every individual, and under similar circumstances, a determinate quantity of matter is separated from the blood for purposes of nutrition, or for the formation of solids; and that another quantity is

[407] On the subject of the antagonism of the secretions, vide particularly the 1st volume of Heusinger's *Zeitschrift für die organische Physik*, S. 149. The whole doctrine, however, stands in need of careful revision, under the lights afforded by Physiology and Medicine as they now exist, occasion being seized to try the various therapeutical procedures which rest upon it in their fitness or inapplicability. On this subject, see farther Physiology in its applications.

[408] [I seize this opportunity to avow myself entirely sceptical in regard to the doctrine of vicariousness of function, as generally understood. I do not believe that any organ of the body either can or ever did supply the place in point of office of any other. One secretion will indeed become contaminated by admixture with the elements of another; but this is from the general current of the circulation, the common source of all the secretions, becoming loaded with these elements: in icterus the serum of the blood is yellow, and so are the urine and the sweat; in Bright's disease of the kidney, the serum of the blood is mingled with urea, and this substance makes its appearance in the fluids accidentally effused into the cavities of the body. Undoubtedly the skin is more active at one time, the kidney at another; but this is merely in regard to the water that is thrown off, not to the characteristic and distinguishing elements of the cutaneous and renal secretions. Strong and healthy persons who are perfectly temperate, even resist the influences that produce what is vulgarly called vicarious action between the skin and kidney in a very great degree. R. W.]

used for the purposes of secretion and excretion. This, even in the normal state, is subject to variation; severe bodily exertion, for example, accompanied by copious sweating, is soon followed by emaciation unless the supply of food be proportionately increased. The same thing happens in all colliquative diseases, in which particular secretions are very much augmented; as, for instance, in severe and long continued diarrhœa, ptyalism, ephidrosis or profuse sweating, &c. &c. Many of the secretions increase and diminish at different times in the normal condition, altering in a quantitative point of view especially; in the colder season of the year, for example, the secretion of the kidney is increased, that of the skin is diminished; in the warmer season, again, the secerning relations of these two organs are reversed. That which here follows upon the dissimilar temperature of the seasons, may temporarily follow an hundred particular circumstances—be consequent upon rest or active exertion, may be produced by the use of particular articles of food or of medicine, by exposure to excessive heat or severe cold, and to morbific influences generally, &c. Upon this principle of a regular antagonism among the excretions, depends one of the most powerful of our therapeutical procedures[409]; we have constant recourse to this physiological law in our treatment of disease.

§ 211. It is indubitable that the secretions are all more or less under a determinate influence of the nervous system. We know that particular impressions upon the nervous system cause essential alterations in the constitution of the secretions. As examples, the implication of the renal secretion in the cold stage of fever, the dis-

[409] As examples may be quoted, the daily practise of acting upon the bowels and skin, with a view to repress the secretion of milk in women who either do not mean to give suck or who are weaning their infants, of prescribing purgatives, diuretics and diaphoretics in cases of dropsical effusions into the internal cavities of the body, or the general subcutaneous cellular tissue. The whole doctrine of the *Crises* in disease may be said to rest upon the physiology of secretion. [In the present state of physiology and pathology we take a somewhat different view of the import of the discharges that occur on the subsidence of acute diseases, and that are called critical. Such discharges in general are little more than evidence of abated morbid actions: these cease, the natural functions of organs return. Still it must be allowed that the secretions are all *excessive* in the first instance; so that there is something more than a simple return of healthy function, which it is not very easy to explain. R. W.]

turbance of the biliary system from violent mental emotions, such as anger and vexation, the plentiful secretion of tears that accompanies grief or joy, the increased flow of saliva on the thought or sight of dainty articles of food, &c. &c[410].

§ 212. The excretory ducts of the secreting glands exhibit proper motions, which are not without influence on the progress of their contents. These ducts are, in fact, provided with strata of contractile fibres, which resemble those of the involuntary muscles, and which contract on the application of stimuli[411].

CHAPTER VI.

OF ABSORPTION, AND THE MORE INTIMATE PROCESSES OF NUTRITION.

General Considerations.

§ 213. The essential part in the entire process of nutrition and secretion depends on the capacity of organic substances, in general, to take up or appropriate, by invisible pores, the vapours and fluids, with which they chance to be in contact. These vapours and fluids then penetrate the parenchyma of organs, make their way to the blood, and by and by appear again, often in other shapes, in the excretory ducts of secreting glands. The process in question is spoken of in physiology under the title of ABSORPTION, one species or form of which is RESORPTION, inasmuch as organic fluids and the solid elements of the animal body liquefied, are again taken up into the mass of its fluids. The TRANSUDATION or penetration of the tissues of the body by elastic fluids or gases, and by liquids, is also to be referred to the cycle of the same phenomenon[412].

[410] On these topics vide the Physiology of the Nervous system, and the General Physiology.

[411] Müller quotes the readily observed fact, that the ductus choledochus of recently killed birds contracts powerfully on the application of a mechanical or the galvanic stimulus. From the structure of the excretory ducts of glands we are enabled to explain various morbid phenomena :—jaundice as a consequence of a spastic state of the gall-ducts, &c. &c. See on this subject the following books of this work.

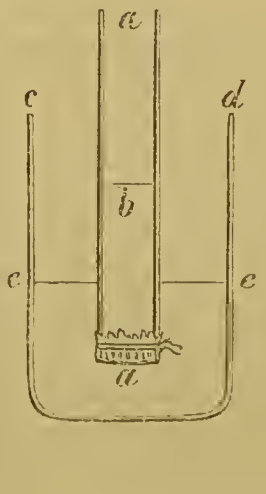
[412] On the entire subject of absorption the works of Magendie deserve to be

Physical Conditions of Absorption.

§ 214. The permeability of the tissues by liquids is sufficiently proclaimed by the fact of their being very generally penetrated by the fluids with which they happen to be in contact. This penetration is a process that is entirely independent of vitality; it takes place through dead animal membranes and tissues, and out of the body, in precisely the same manner as it goes on in the living organism. In its course many interesting physical phenomena present themselves, which have been spoken of under the names of *endosmose* and *exosmose*, and which are susceptible of illustration by very simple experiments[413]. The primary phenomenon is this—that

particularly eonsulted. See his *Physiology*, and his *Lecons sur les phenomènes physiques de la Vie.*

[413] Dutroehet investigated these phenomena more earefully than had yet been done, [by Porret in 1816 and Fiseher of Breslaw in 1822,] and designated them by these namcs. Vide his eolleeted treatises on the subjeet: *Mémoires pour servir à l'Histoire Anatomique et Physiologique des Vegetaux et Animaux*, Paris, 1837. Berzelius has given an excellent eondensed view of the subjeet of endosmose and exosmose: " The phenomena exhibited by bodies in solution in traversing solid living parts, do not depend solely on the properties whieh bodies in solution have of diffusing themselves evenly through the fluids whieh are their menstrua; the animal membranes and the water eontribute their share, inasmueh as the water passes with the dissolved substanee, and from this results a phenomenon whieh in its effects resembles in every respeet an absorption. For the sake of illustration, let *a a* in the aeeompanying eut be a tube open at both ends, but having a piece of moist bladder tied around its lower extremity. Let a solution of any salt be now poured into the tube, and this be plunged into a



substances which are soluble in water and various other fluids make their way through animal membranes along with their menstrua;

larger vessel, *c d*, containing water, the tube being immersed till the solution, *a b*, is at the same level, *e e*, as the water in the outer vessel, *c d*. After a little time it will be found that the fluid in *a a* has risen and got above the level *e e*, to *b*, for example, and that it is continuing to rise, and will go on rising, until the two fluids on the opposite sides of the bladder are of the same density, so that if the tube, *a a*, be not of sufficient length, the fluid may even run over, having filled it completely. If the tube, *a a*, instead of containing a saline solution contain water, and the recipient, *c d*, instead of water contain a saline solution, things being disposed as before, the fluid in *a a* far from rising will begin to fall, and instead of falling in *c d* it will begin to rise. When the tube and the recipient contain solutions of different salts respectively, but as nearly as may be of the same density, the level of the fluid in neither will be altered perceptibly; but after a certain time the two salts will be discovered mingled together in both the tube and the recipient, or in the fluid on both sides of the bladder. If the densities of the two saline solutions have been different, the surface of that which is the more dense will rise, that which is less dense will fall; but it will be found, nevertheless, that from the solution of greatest density a portion will have passed into that of least density; the penetration has not therefore been all one way, but reciprocally from each to the other, only in greatest measure from the less to the more dense fluid. This phenomenon does not take place only when moist animal membranes are the intermedia between the two heterogeneous but miscible fluids; it also occurs when the interposed body is of an inorganic nature, but thin and porous, and possessed of strength enough to support the increasing column of the denser fluid—such as thin slices of slate, earthenware, &c. In general it may be said that the power of producing the phenomenon in question belongs to all bodies which can absorb and retain a fluid in extremely delicate pores. Poisson has offered a mathematical explanation which represents the cause of the phenomenon, and which, on the whole, confirms the idea already emitted by G. Magnus, viz., that the attraction between the particles of a saline solution is composed of the mutual attractions of the water and the salt, and of the reciprocal attraction of the molecules of each of these bodies considered apart. These attractions combined are more powerful than that of the particles of water for one another: whence it follows that the water must pass by so much the more easily athwart the pores of an animal membrane, or any other porous interposed body, as it contains less of any foreign substance dissolved in it. But when the membrane or porous body separates two watery solutions (or a watery solution from pure water) in both of which the attraction between the parts is unequal relatively, and the liquids, moreover, exert a reciprocal attraction for one another and at the same time an attraction with reference to the pores of the bladder, it follows that one is attracted with greater force by these pores than the other, and that consequently the quantity absorbed must be proportion-

and farther, that fluids of different densities, contained in receptacles or canals of the body, make their way through the interposed membranes, and penetrate each other mutually, or suffer an interchange of elements, but always with this peculiarity—that the constituents of the more dense fluid mingle with those of the less concentrated fluid in smaller quantity; the constituents of the less dense fluid, on the contrary, especially its water, making their way in larger proportion to the more dense fluid. This interchange of elements or mutual penetration of the two fluids goes on until both have acquired the same degree of density or spissitude. The thickness of the membrane, the laxness or denseness of its texture, exert a certain influence on the phenomenon in question; still, under all circumstances, it goes on, and in this way it is that an interchange of fluids is effected in the living body;—one matter is taken up, another is given out. It is even probable that very finely divided and merely mechanically suspended corpuscles may make their way through lax tissues, and then be deposited in distant parts[414].

Phenomena of Absorption.

§ 215. That many substances make their way into the blood by imbibition, is readily proved by experiments of the simplest kind. Let a small cut be made into the skin of the back of a frog, and

ally greater on one side than on the other, after which the fluid which is on the opposite side of the membrane attracts that which had penetrated into this last, and mingles with it. From thence result the two currents athwart the membrane, of which that of the least dense or more watery is more rapid than that of the more dense or least watery fluid. (*Chimie*, 4te Aufl. B. ix. S. 161.)

[414] Many facts seem to give us assurance of this; for example, the finely divided molecules of mercury contained in mercurial ointment, which, according to my own measurements, are often under $\frac{1}{1500}$th and $\frac{1}{2000}$th of a line in diameter, rubbed upon the healthy surface, make their way into the blood. I have also, in a particular instance, observed the absorption of the fine particles of a metallic pigment; this was in the body of a soldier, upon whose right arm there was a large red tattooed figure, apparently of ancient date,—the body had been sent to the dissecting room from a house of correction. The lymphatic glands of the axilla were found of an intense red colour, from the deposition of cinnabar in their texture. This could have been derived from no other source save the tattooed part. This fact is also evidence of the absorbing powers of the lymphatic vessels.

through this a few drops of a watery solution of strychnine be infused; in a few minutes the animal will be observed to be seized with convulsive twitchings, which increase in violence, and by and by end in complete spasm or tetanus of the whole body[415]. This experiment may be varied in different ways, and the several tissues tried as to their capacities of absorption. The different degrees of this capacity seem to stand in relation to the greater or less vascularity of the tissue. The external integument, so long as it is covered with the epidermis, absorbs with extreme slowness[416]; the epidermis removed, however,—by means of a blister, &c,—and the vascular lamina of the corium exposed, absorption goes on with great rapidity. It is upon this fact that what is called the *endermic* method of exhibiting medicines depends. Mucous membranes and serous membranes possess the absorbing faculty in great perfection[417]. The coats of vessels of all kinds are farther highly permeable to all man-

[415] The best article for all such experiments is strychnine; its effects are striking, and not being volatile, it can be used without danger. The greatest care is nevertheless at all times necessary,—the skin of the fingers must be whole, and wounds and punctures are particularly to be avoided. A solution of five grains of nitrate of strychnine in an ounce of distilled water is well adapted for making experiments.

[416] This, at all events, is the case with the human skin. Animals with smooth and muco-membranous-looking skins, frogs for example, absorb watery fluids much more rapidly. If a frog be introduced into a narrow cylindrical vessel, over the bottom of which a small quantity of a solution of strychnine has been poured, so that the hind feet or toes of the animal only are in contact with the poison, indications of its specific effects will speadily appear. Or if a solution of ferrocyanate of potash be employed, as Müller proposed, the absorption of some portion of this substance can be made manifest by the use of reagents,—the lymph from under the skin of the back assumes a blue colour on the addition of a solution of a salt of iron. On the subject of absorption by the uninjured skin see an account of the experiments of Berthold in Müller's *Archiv*, 1838, S. 177. After immerson in a bath for a quarter of an hour, he found that his body had gained 171 grains in weight; after an hour's immersion it had gained 510 grains.

[417] Symptoms of poisoning follow with the greatest rapidity when a solution of strychnine is thrown into the cavity of the thorax; a dog or a rabbit being the subject of experiment, these symptoms generally present themselves in from one to two minutes. Solutions of coneïne, used, in the same way, are very potent; a drop or two applied to the conjunctiva of a rabbit induced violent spasms and death in the course of from three to four minutes. Vide Pohlmann, *Physiologisch-toxikologische Untersuch. über das Coneïn.* Erlang. 1838.

ner of watery fluids. Experiments with poisons show that absorption, in the sense of *simple imbibition*, is a purely physical or mechanical act, and that poisons are taken into the circulation without anything like elective affinity in the parts, as they are in what may be called *organic absorption*, of which I shall have to speak immediately[418].

§ 216. The vessels by which absorption is effected are the veins and lymphatics. The absorbing faculty of the veins is vouched for by the experiments adduced in the preceding paragraph; but it is easy by direct experiment, by the complete isolation of one of the veins, to demonstrate the power of absorption possessed by this class of vessels[419]. For the absorbing faculty of the lymphatic vessels, the assumption of the chyle by those of the intestinal canal, gives ample assurance. It is otherwise highly probable that *organic absorption*,

[418] That the effects of poisons follow their reception into the circulating system can be demonstrated by very simple experiments. It matters not how or where the strychnine is applied to the frog's body—it may be insinuated into a wound, thrown into the cavity of the thorax or abdomen, applied to the external surface, or injected into the stomach, the poisoning follows in every instance, only with different degrees of rapidity; cramps and tetanus ensue with the same certainty, if the animal be decapitated before the application of the poison; but if the heart be cut out before the poison is infused beneath the skin, the frog will continue to live for hours without showing a symptom of the specific effects of strychnine. Magendie found that a poison applied to a bare nerve had no influence on the general system of an animal; Wedemeyer saw no effect from the application of concentrated hydrocyanic acid to a bare nerve.

[419] Magendie having laid bare the jugular vein of a dog, and dissected it free from all surrounding connexions, found that on applying a watery solution of the extract of nux vomica to its outer surface, symptoms of poisoning supervened in from four to ten minutes, according to the size and strength of the animal. Magendie demonstrated the absorbing powers of the veins by highly ingenious experiments. He stupified a dog with opium, and then separated one of the legs from the body all to the principal artery and vein of the limb; these were carefully cleaned, the cellular membrane which surrounded them, and which might perchance contain lymphatics, being removed; two grains of the upas poison were then inserted under the skin of the foot: the effects were as rapid and as powerful as in cases where the extremity was not separated from the rest of the body; in four minutes symptoms of poisoning were apparent, and before the tenth minute had elapsed, the animal was dead. To remove all grounds of cavilling, to prevent the possibility of any lymphatic vessels being still left within the coats of the artery and vein, Magendie repeated the same

which presumes a specific activity in certain vessels, is performed by veins as well as lymphatics. Fluids received into the stomach, and certain matters in the intestinal canal, colouring matters, for instance, and many salts, seem not to be taken up by the lacteals, but by the veins[420]. That the veins of the lungs absorb is demonstrated by the effect of poisonous vapours received by inhalation; this is probably the channel by which miasms and contagions dissolved in the air make their way into the organism[421]. It is impossible to conclude in many cases whether the veins or the lymphatics are the agents in absorption, the absorbing faculty of these last has indeed been recently called in question altogether[422]. Many of the phe-

experiment, but with this difference: the artery and vein were both divided, and the continuity of their canals was restored by means of barrels of quills, with which the vessels at either end were connected by ligatures. The upas poison inoculated into the paw produced its known effects in the usual time, that is to say, after the lapse of about four minutes. The assumption of the poison by the veins was also proved by this: that compression of the walls of the vein prevented the effects of the poison proceeding farther after they had begun to appear; they were again manifest when the vein was left free, and again they were restrained when the compression was renewed. Vide Magendie, *Elemens de Physiologie.*

[420] Tiedemann and Gmelin found colouring matters which had been taken into the stomach in the blood and in the urine, but never in the chyle. They also rarely observed salts of any kind to be taken up by the lacteals. Vide their researches into the ways by which matters get into the blood from the stomach and intestines (*Versuch über die Wege, &c.* 1820.) In all experiments of this kind it is obvious that substances can only reach the greater circulation in a roundabout way. They are poured by the cæliac and other intestinal veins into the portal vein; from this they are transmitted to the hepatic vein, and by this they reach the vena cava.

[421] Many cases of poisoning have occurred by the inhalation of poisonous gases and vapours, arseniated hydrogen, for example, which seem to make their way into the blood through the unbroken vascular membrane with the same certainty and ease as when they are injected directly into the veins.

[422] To this are referred a number of pathological phenomena, for example, the absorption of the colouring matter of the bile from the skin in jaundice, of the water in anasarca, &c.; in these cases it is generally assumed, but upon no sufficient grounds, that the absorption is effected by the lymphatics. We have better evidence of their action under other circumstances, after wounds received in dissections, for example, after infection with the syphilitic virus, &c. when inflammations of the lymphatic vessels and glands are very common,—though inflammations of the veins are at the same time frequent also. All these phe-

nomena of absorption are, it must be owned, extremely mysterious, the shrinking and disappearance, for instance, of parts that have no lymphatics, the removal of solid bone in consequence of mechanical pressure, &c[423].

§ 217. Neither anatomical nor physiological considerations render any satisfactory account of the import and office of the lymphatic vessels. Their roots or mode of origin, and in part their course, are unknown to us. As to their office, it is commonly said that the constituents of the blood which are dissolved in the liquor sanguinis or plasma—the albumen and fibrine—transude the walls of the finest capillaries, and bathe or come into immediate contact with the parenchyma of all the organic parts; the greatest proportion of the fluid shed is believed to be used up either in nourishing the parts or in furnishing the secretions; that portion of the fluid which is not expended in these directions, and which, therefore, seems to be superfluous, is believed to be collected by the net-work of lymphatic vessels which is supposed to form an element in the intimate structure of all the tissues, and to be returned by the thoracic duct to the blood[424].

nomena are, however, susceptible of explanation in another way. The means by which the absorption of pus is accomplished are unknown; the pus-corpuscle as such cannot be taken up; probably the mere serous part with the pus-molecules suspended or dissolved in it is absorbed. Magendie denies, or at all events greatly doubts, absorption by the lymphatics, and is disposed to ascribe this function entirely to the veins. See note (414) to § 214.

[423] Among phenomena of this kind are to be reckoned: the disappearance of the fat in old age and in the course of diseases; the normal disappearance of the thymus from and after the second year of existence, the organ having attained its maximum development in the course of the first year during the period of suckling; the absorption of parts that are not properly organized, or of the roots of the milk-teeth during the development of the permanent set, the disappearance of bone in consequence of pressure, as of the skull in cases of fungus of the dura mater, of the sternum and ribs in aneurysms of the aorta, &c., and in atrophy of the tissues in general.

[424] All who have given their attention to the department of anatomy connected with the subjects just alluded to, are aware of the difficulty and obscurity which surrounds it. Our knowledge of the lymphatic system is chiefly grounded upon artificial injections with mercury, which are at all times extremely deceitful, and liable to lead into error. The accounts of the very best observers must here be received with diffidence. I make no exception in favour of those even of such

Nutrition and Growth.

§ 218. *Nutrition* and *growth* are connected with precisely the same anatomical and physical conditions as absorption. The source of all nutrition and of all growth is the blood, from which materials are shed or separated to be employed in the formation and renovation of the tissues. This is obviously only to be effected by the parenchyma imbibing from the capillaries and intermediate vessels. The walls of the most delicate vessels are, in fact, as competent and disposed to permit the escape of the plasma or liquor sanguinis, charged with the elements of nutrition, from within, as we have seen them apt to be penetrated from without by fluids holding various substances in solution. We have evidence enough of the occurrence of *ex*udation, the opposite of *in*sudation or absorption; but both one and the other are connected with the same physical peculiarity of the tissues, a peculiarity which is farther most intimately allied to secretion. The transudation of vapours, *exhalation*, as well as that of fluids, *exudation*, takes place in conformity with the laws of imbibition,—*endosmose* and *exosmose*.

men as Fohmann and Panizza, whose preparations preserved in the Museums of Heidelberg and Pavia, closely inspected, have rather tended to increase than to diminish my doubts of the correctness of their ideas. In the majority of instances we have no kind of security that canals accidentally made in the cellular tissue by the pressure of the column of mercury, are not described as lymphatic vessels, or that the cellular sheaths of blood-vessels filled in the same way, are not viewed as lymphatic trunks. It is very remarkable that in all the transparent parts of animals in which we are in the habit every day of observing the circulation, and in which, according to the statements of the anatomists particularly named, and others, numerous and dense net-works of lymphatic vessels are present, we should never discover any vessels circulating lymph. Lymphatic vessels, were they present in fact, would certainly be visible from the nature of their contents and the form of the globules they include. It is only among those amphibia, as for example, the turtles, where the lymphatic vessels are very greatly developed, and where in their course we find pulsating hearts from which lymph can be collected in large quantity, that the observations of late anatomists receive support. No department of anatomy seems deserving of so careful and comprehensive a review as that which bears reference to the lymphatic system. Without accurate anatomical knowledge there is no taking a single assured onward step in physiology.

§ 219. The oozing of fluids through the tissues takes place after death as a purely physical phenomenon. In the dead body we constantly find that the bile has made its way through the walls of the gall bladder, and stained the organs in contact with it of a yellow colour. Transudations, or effusions as they are called, are constantly occurring in the course of diseases, in dropsies, for example, in which a watery or serous fluid permeates all the tissues and collects in quantity in the areolæ of the cellular substance and in the serous cavities of the body. Exudations are frequent consequences of inflammation. In the course of respiration, water in the form of vapour, combined with, or holding carbonic acid gas in solution, permeates the vessels of the lungs and the delicate membrane of the pulmonary cells; many odoriferous or strong smelling substances are also readily to be detected in the exhalation of the lungs[425]. Every cold we catch shows us how rapidly watery fluids can permeate the mucous membranes[426]. But as in every other process of the living organism, transudation does not any more than absorption take place in conformity with merely physical laws, else would the fluids with all their dissolved matters transude universally, and in the same way, would the extent to which transudation occurred be regulated only by the varying density or permeability of the tissues. It would appear that in the normal, as in abnormal or pathological

[425] Diluted spirits of all kinds, æther, camphor, oil of turpentine, &c., &c., injected into the veins or taken into the stomach, are in part at least thrown off again by the lungs; their presence is immediately proclaimed by the smell of the breath. A few grains of phosphorus dissolved in oil and thrown into the femoral vein of a dog, by and by induces the exhalation of a thick white vapour from the nostrils, which consists of phosphorous acid, and shines in the dark. Vide on these topics the *Physiology* of Magendie, and Tiedemann's *Zeitschrift*, B. v. S. 203.

[426] The fluid which often distils from the nose in such profusion during the first stage of a catarrh, appears to be a pure transudation from the vessels of the Schneiderian membrane. It consists in great part of water, with a small quantity of albumen, which may be coagulated by the addition of alcohol. Not a trace of mucus is discoverable in it; neither do we observe any mingled epithelial cells. The dissolved saline matters—mostly common salt—shoot into their appropriate crystalline forms on the glass plate upon which a drop is made to evaporate. The mucus gradually returns as the secretion becomes thicker; and now numerous epithelial cells in a state of transition into pus-corpuscles and veritable pus-corpuscles make their appearance.

processes, certain substances only make their way from the blood through the membranes, sometimes albuminous fluids only, as in dropsies, sometimes fibrinous fluids, as in the plastic exudations of inflammation. Foreign substances taken up into the blood, many colouring matters, for instance, unless they be speedily discharged again through the kidneys, are deposited in certain parts or tissues of the body[427].

§ 220. In the process of nutrition we are forced in the present state of physiology to recognize an exudation of matters from the blood, and the deposition of these in the parenchyma of organs. Nutrition in vascular parts is effected apparently by the plasma transuding the parietes of the peripheral vessels, and so bathing the islets of the parenchyma immediately. At an earlier period it was supposed that blood-globules were deposited entire, and growth and nutrition effected in this way; or otherwise, it was believed that the nuclei of the blood-discs, or the blood-discs themselves, became aggregated like strings of beads in order to form particular tissues, the muscular tissue in especial[428]. These views are, however, all alike untenable; to the best of our knowledge the blood-discs seem rather to take no direct part in the business of nutrition; their office

[427] If an animal have certain colouring matters, such as madder, mixed with its food, the bones after the lapse of a few weeks are found of a decided red colour; when the madder is left off, the colour fades and by and by disappears (the colouring matter has been absorbed.) In the same way it has been repeatedly observed that the continued use of nitrate of silver internally is followed by a dusky leaden grey or slate colour of the skin, which only disappears very gradually, never save in the course of years. The salt of silver appears to be deposited in the skin and chemically combined with the organic substance. [The colouring matter of the carrot used as a daily article of food for some time stains the human skin of a deep yellow, that of coffee makes it brown, &c.. R. W.]

[428] Doellinger believed that in young fishes he had seen an apposition of blood-corpuscles, as also a disintegration of individual particles of the granular parenchyma of organs, and a transformation of these into blood-corpuscles. See his paper on the circulation, &c., in the *Trans. of the Munich Academy*, vol. VII. and his work on secretion (*Ueber Absonderung*, 1819.) No observer since his time who has made use of a good microscope has been able to see anything of the kind. [This was the case till the present year (1842), which has witnessed a revival of Doellinger's notions by Dr. Martin Barry, who appears inclined to view the blood disc as the immediate agent in the construction of many tissues, particularly the muscular, the elementary fibre of which (designated a spiral fibre) may, according to Dr. Barry, even be detected in the nucleus of the blood-

is not [certainly] known to us; but we might presume that they bear the same relation to the plasma and its normal composition as the cellular parts of the secreting glands do to the secreted fluids[429]. It seems

disc. This view of the mode in which the tissues are formed, is certainly too mechanical, and is I believe at variance with sound physiology. In the same way as we see the surface of a fresh wound forming cells (exudation corpuscles) as a means of reparation, out of the liquid plasma that oozes from it, so, very certainly, do the muscles and all the other tissues of the body form their constituent cells and fibres from the liquid plasma which permeates the capillary vessels in their vicinity and bathes them. The blood-corpuscles themselves are but transition forms, means to a specific end, free secreting cells, their secretion being the plasma or general formative fluid. (See addition to next note.) From the statements of M. Magendie, (Lectures, in the *Lancet*, 1838-39, vol. i. p. 255,) it would seem that a mere clot of fibrine is a solid having a certain structure; a view which is confirmed by the observations and figures, contributed to Gerber's *Anatomy*, by Mr. Gulliver, (p. 30 et seq.; Appendix, p. 14,) who depicts fibrils, organic germs or cell-like objects, and granular matter, in fibrine which has set simply from death; he has also shown the same structure in false membranes (loc. cit. fig. 272). In a clot of fibrine, then, there is a curious structure which is not less complicated than that of many permanent tissues—a fact which should not be lost sight of by those physiologists who may be disposed to refer either growth or nutrition to the immediate mechanical agency of the corpuscles of the blood.

The important discoveries of Schwann as to the origin of all the tissues from cells should be especially examined in relation to these primordial fibres in fibrine. Mr. Gulliver never saw any evidence of their being altered cells; indeed the fibres appear so quickly after coagulation, that he may well ask how their origin can be accounted for upon Schwann's theory. See Gulliver's Contributions, &c., *Lond. and Edin. Phil. Mag.* for Aug. Sept. and Oct. 1842. R. W.]

429 I shall have occasion by and by to speak of the influence which the blood-discs may have in acting as a stimulus upon the central parts of the nervous system. It is for the rest very possible, nay extremely probable, that the blood-corpuscles exert a direct influence upon the constitution of the blood *(die Blutmischung.)* [In the sentence to which this number refers, I have transposed a couple of lines from the notes to the text, inasmuch as they seem to me to contain the essence of an important discovery which belongs of right to our ingenious author. Turpin spoke of the blood-discs as peculiarly organized bodies, possessed of a power of absorption, assimilation, and growth, and having a certain determinate period of existence; Hünefeld compared them to the ova of birds: Schwann regarded them as equivalent to the cells of the animal tissues generally; and Valentin to the nuclei of cells; but Dr. Wagner is, I believe, the first who has said in express terms that the *blood-discs bear the same relation to the plasma*

very probable that the stream of plasma which is in contact with the walls of the vessels (§ 122), and in which the lymph corpuscles swim, stands in intimate relationship with the nutrition of the tissues; the slowness of its motion through the capillary vessels must facilitate its transudation through the delicate walls of the containing channels. The absence of these lymph-streams in the vessels of the lungs testifies in favour of this idea (§ 123.) The un-vascular, or as they used to be regarded, un-organized parts and tissues, also depend for their growth and nutrition upon the blood[430]. All these tissues,—the epidermis, the hair, the teeth, the crystalline lens, the epithelia—are ministered to by some element of the blood: they every one consist of cells[431]; their growth takes place by apposition; the cells which lie deepest or nearest the blood-vessels are constantly being renewed, and are largest, softest, most perfect, and frequently full of fluid derived from the blood; whilst the more remote cells become dry, and are pushed onwards and in many cases cast loose and detached,—the epidermis and epithelia, for example, are in a perpetual state of renovation, the outermost layers exfoliating continually. The layers of these tissues which lie nearest to the capillary vessels are consequently nourished essentially in the same way as the other more highly organized and more vascular tissues, such as the muscles, the nerves, &c[432].

and its normal composition as the cells of secreting glands to their secretions (*Lehrb. des Physiol.* 2te Abth. Leipz. 1840.) The same idea is propounded by Henle (*Allgem. Anatomie*, Leipz. 1841), who, in speaking of the blood-discs says (op. cit. p. 460): They may be regarded as *suspended glandular corpuscles*, which take up a certain matter from the plasma [chyle], alter it in all probability, and restore it when duly prepared to the plasma, they being themselves dissolved. In this way we can understand how they, though not the directly nutrient, are still the vivifying element in the blood." At p. 979 he reverts to this subject in these words. "I have already spoken of the blood-corpuscles as floating glandular cells, and can illustrate the function of the cells of glands by their means: As the blood-corpuscles arise in the blood, or more properly in the chyle, so do the cells of glands arise in the nutrient plasma," &c. See in connexion with this interesting topic my Annot. No. 406. R.W.]

[430] The older division of tissues into organized and unorganized is rendered inadmissible by the recent advances of histological knowledge: all the tissues are organized.

[431] The cellular structure of hair is beautifully seen in that of the deer kind. The pigmentary cells from the choroid coat of the eye are also excellent subjects for the study of the cellular character.

[432] [It is easy enough to explain the escape of fluids, from their containing chan-

§ 221. In nutrition we observe the same remarkable circumstances as in resorption and secretion, viz: the specific transformation and deposition of determinate substances in determinate situations. Every tissue, every organ attracts from the blood particles similar to itself, or metamorphoses the proximate principles of the blood into its own elements. The chemical constitution of the different tissues shows, however, that their proximate principles are already in part present in the blood, fibrine for example, of which the muscles consist almost entirely, and albumen, which is contained in so many of the tissues. Still, in the deposition of the elements of the blood in the tissues, other and various combinations of its primary constituents and radicals are encountered just as they are in the secretions. This deposition and alteration of the constituents of the blood, this contribution and transformation of its elements towards the integrity and perpetual regeneration of the tissues, of course proceeds so slowly as entirely to escape observation. The process, however, varies greatly according to age, constitution, idiosyncrasy, state of health, &c. It is most rapid in youth, during the growth of the

nels for the purposes of nutrition and vital endowment: the push of the heart and the spongy texture of the minuter arteries suffice for this. It is much more difficult to give a reason for the return of the plasma so exuded, contaminated doubtless with the re-liquified effete particles of the body, into the venous circulation. In fact, no explanation of the way in which this return is effected has ever been offered. My views and observations lead me to ascribe it among all the more perfect animals to the influence of the cutaneous exhalation, which in causing a difference of density between the outgoing and incoming currents of blood, secures the conditions necessary to the endosmotic flow towards the veins, of the existence of which our experiments with poisons afford us such indubitable evidence. I have shown in my portion of Annot. 342, that the serum and blood of the current flowing towards the heart is of greater density than that which is leaving it. The quantity of water thrown off by the human skin in a day amounts to upwards of 30 ounces as a mean, about as much, consequently, as is got rid of by the kidney; by the whole amount of the water thus eliminated from the skin, however, must the venous blood of the peripheral parts of the body be more dense than the arterial blood, and in the ratio of its greater density must be the force of the endosmotic stream from the areolæ of the tissues towards it in its containing channels. The lymphatic system I hold subordinate to the same end; it is developed in the ratio of the impermeability of the general integument of the body, ex gr. among the lizards, crocodiles and tortoises. I shall not pursue this topic farther here, but beg to refer to a short Essay which I have prepared and mean immediately to publish on the Special Functions of the Skin. R. W.]

body; it is greatly less in old age; but it differs widely with reference to particular organs. Morbid conditions of the most different kinds, too, such as profuse hemorrhages and diarrhœas, fevers, excessive bodily and mental efforts, the depressing affections, such as care and sorrow, &c. are all incompatible with perfect and powerful nutrition, and induce wasting of the several organs. In simple hypertrophy and atrophy of individual organs, we have instances of nutrition locally increased and diminished[433].

§ *222.* The circumstances connected with the nutrition of the fœtus are in some sort peculiar. We have seen (§ 81 note) that in man and the mammalia there is no direct vascular connexion between the parent and the embryo. The highly developed capillary vessels of the fœtal portion of the placenta form loops which are enclosed in villous processes and surrounded by a delicate membrane. These are bathed by the blood of the mother, and it is here that an interchange of matters is effected. The entire anatomical structure and the growth of the fœtus, explicable in another way, lead us to conclude that the vessels of the fœtal placenta absorb matters from the blood of the parent in conformity with the laws of endosmose and exosmose, and that these matters are expended on the growth and maintenance of the fœtus. Lymphatics have not been certainly demonstrated in the umbilical cord and placenta, so that the umbilical vein must be the channel by which the nutrition of the fœtus is accomplished.

[433] The diminished nutrition that accompanies profuse discharges may be explained from the abstraction of elements from the blood which would have been expended for purposes of nutrition. In febrile diseases with diminished secretion, again, the defective nutrition may depend on the indisposition to take food, and the tardy and imperfect digestion which any that is taken undergoes. (§ 135 note.) That the more rapid circulation in inflammatory and nervous fevers can have any influence in the direction indicated, by preventing the due exudation of plasma and consequent deposition of nutritive matters, is an idea which cannot be entertained. [Surely the explanation is not difficult here: in febrile and inflammatory diseases, one of the processes that most rapidly consumes the body is even increased in energy—the respiratory process; but as food cannot be taken, or if taken cannot be digested and assimilated, and as the oxygen of the inspired air must combine with carbonaceous matter, if life is to continue, it seizes upon and consumes the carbon of the body itself, which therefore and of necessity wastes; the body may be then likened to a cistern from which the supply has been cut off, whilst the tap is left running. R. W.]

§ 223. All the materials expended in the nutrition of the body are derived by the blood from the food, which is with perfect propriety spoken of as more or less nutritious. From the food, however, are derived only the elements of the tissues and the proximate principles of the body. These consist especially of albumen, fibrine, hæmatine and globuline and fat; in the whole of these substances save the last, azote is a constant and necessary ingredient,—it is present in them all in considerable quantity; they are also very rich in carbon, less so in oxygen, and poor in hydrogen. The whole of them as well as the inorganic constituents of animal bodies exist in the generality of alimentary articles, whether derived from the animal or vegetable kingdom. It would seem that the most perfect nutrition implied the necessity of a certain variety and change in the articles of aliment: the various compounds which make up the body, require supplies of differently compounded substances for their maintenance and regeneration. Hence the general advantages of a mixed diet of animal and vegetable substances of good quality and in adequate quantity; this is unquestionably the diet upon which the health and strength of man in all the temperate zones of the earth are best maintained. On the same grounds is milk an article of sustenance, which from its composition, from its containing all the substances in due proportion that are required to preserve and restore the constituent parts of the organism—caseine, (which represents fibrine and albumen) fat, sugar of milk, and all the extractive matters and salts which are found in the animal fluids—is competent by itself to maintain the body for a long time in its integrity[434]. Almost every other article, how digestible

[434] Dr. Prout showed, in a very ingenious manner, that all alimentary matters might be referred to three great classes—a saccharine, an oleaginous, and an albuminous class. The saccharine class is derived especially from the vegetable kingdom, and consists almost exclusively of carbon and oxygen, with a small proportion of hydrogen; oils and fats are rich in carbon and hydrogen, and contain much less oxygen than sugar; albumen, besides carbon, hydrogen and oxygen, contains a notable quantity of azote. But the principal constituents of milk—sugar of milk, butter, and caseine—represent precisely the three classes into which food of every kind may be arranged. See his very able treatise, *Chemistry, Meteorology and Digestion*, 8vo. Lond. 1834. [Another and more physiological division of alimentary matters were probably into a carboniferous and an azotiferous class, the carboniferous standing in relation to the respiratory

soever it may be, is known to be inadequate without additions to nourish the body and support life for any length of time. This is a fact that has been demonstrated by direct experiments[435].

NUTRITION OF VEGETABLES.

§ 224. It is a matter of great interest to compare the nutritive processes of vegetables with those of animals. The process of assimilation in the plant is much more simple than in the animal, and consequently much more easily followed in its chemistry and mechanism[436]. We have already spoken of the formation and circula-

proeess or the generation of heat, the azotiferous in relation to the maintenance of the various tissues of the body at large. To the first elass we should refer starch in all its shapes, sugar, gum, oil and fat ; to the seeond, vegctable and animal fibrine, albumen, and easeine cspeeially. R. W.]

[435] Consult the interesting experiments of Magendie, in his *Elements of Physiology*. Dogs, when fed on sugar and water alone, wasted rapidly, became extremcly weak, and died in from four to five weeks; fed with oil, gum, or butter alone, the result was the same, or life was not protracted for more than a few days longer ; these articles are all reeognized as digestible, and they are nutritious when taken along with other substances ; but they eontain no azote, and are innutritious when used alone. The most highly azotized articles, howevcr, whcn given without admixture—such as eheese and hard eggs, are found inadequate to minister to health and long life ; animals restrieted to such diet live long indeed, but they soon beeome weak and lean, lose their coats, &c., the nutrition evidently suffering greatly. All this spcaks loudly against uniformity of food as a dietetic rulc ; sameness is to be avoided as much as possible, and articles of different kinds are to bc mixed altogether. [In Ameriea it is known that a pig will become poor, and even starve, if kept upon apples, pumpkins, or potatoes alone, but that it will fatten if it have a mixture of the three. It is the samc with most other articles of food. Whcre man is eonfined to animal substances alone, as he is in the extremc north, the food is very fat ; fat is here the rcpresentative of the saecharine, gummy and amylaeeous principles, whieh are such important articles of sustcnance over three fourths of the earth's surface. In restricting diabetic paticnts to animal food, it is very important that this be fat, not lean, as it is commonly dircctcd. Bacon, brisket of beef, and brcast of mutton, are the articlcs or parts to be reeommcnded, not rump-steaks and mutton-chops. R. W.]

[436] See the very remarkable work of Licbig, "*Organic Chemistry in its Applications to Agriculture and Physiology*," cd. by L. Playfair, 8vo. Lond. 1840, which mcrits the most carcful study of the physiologist. The statements in the text may bc viewed as very bricf abstracts from this publication. Unfortunatcly

tion of the sap in vegetables, § 107. Vegetables absorb fluids alone, or matters in a state of solution. The crude sap which they derive from the soil through the roots, consists in great part of water strongly impregnated with carbonic acid.[437] This carbonic acid dissolved in the water accompanies the crude sap in its course through the whole plant, fills the cells, the intercellular canals—every part, in a word. In the cells the sap which has now undergone a certain amount of elaboration is also in motion, rising and falling along their walls (the rotation of the cellular sap, § 107). Here, in contact with the substance of the plant, it is that the consolidations and assimilations, the various excretions and depositions

we possess no parallel work on the assimilatory processes of animals. The work of Prout cited in Annot. 434 alone glances at the subject under the same point of view. Any succeeding treatise must unquestionably follow in the path so happily struck out by Liebig, and be grounded on the reciprocal chemical relations between the matters consumed as food and the particles of the body. [The gap here pointed out has been very recently filled by a second work of the Professor of Giessen: *Organic Chemistry in its Applications to Physiology and Pathology*, by Justus Liebig, edited from the MS. by W. Gregory, M.D. 8vo. Lond. 1842. Occasion has already been taken by the translator and editor of this work to refer to the interesting views of Liebig in connexion with the subject of assimilation. Annot. 224. R. W.]

[437] The absorption by vegetables of carbonic acid from the atmosphere, through the medium of the soil, had already been demonstrated by Saussure, Ingenhousz, Priestley, Sennebier and others. The leaves and all the green parts of plants possess the property of abstracting this gas from the atmosphere; even detached portions of plants have the same remarkable faculty; a slip of a plant put into a jar containing water impregnated with carbonic acid, soon removes the whole of it; [the branch of a vine confined in a glass tube in bright sun-shine, will completely absorb a considerable stream of carbonic acid, introduced at one extremity of the tube, fixing the carbon and liberating the oxygen.] The greater number of vegetables derive the carbonic acid which they require as food from the soil in which they grow; a principal part of most soils, however, is humus, a substance which consists of organic, especially vegetable, particles in a state of decomposition; humus in contact with the air has the power of converting its oxygen into an equal volume of carbonic acid gas; with the disappearance of the oxygen, the process of decomposition ceases. [Probably the most prolific of all soils is that formed by decomposing lava, which contains little or no humus; but it has the salts which vegetables most crave in abundance, and stimulated by these the air supplies them with the carbon and azote which they require in addition to enable them to flourish with the greatest luxuriance. Vide Liebig's *Vegetable Organ. Chemistry*, sup. cit. R. W.]

that constitute the nutrition of the vegetable, are accomplished; here it is that the various proximate principles of vegetables, the sugar, gum, starch, &c. substances which contain all the elements of the woody fibre, are prepared or produced[438]. The principal mass of every vegetable, however, consists of carbon and the elements of water, which are present within the vegetable in the same proportions as in water itself. Vegetables receive their carbon from the carbonic acid dissolved in the water which is absorbed by the roots, and this again is derived from the atmosphere and the decomposing humus of the soil. In fixing the carbon, there must of course be an extrication of oxygen; and this gas vegetables actually give off abundantly in bright day-light and sunshine[439]. For every volume of carbonic acid that is fixed by vegetables, the atmosphere receives an equal volume of oxygen gas. This simple assimilation of carbon by vegetables has been demonstrated by unquestionable experiments. It is even as easy to indicate the origin of the other elementary matters which enter into the composition of vegetables. Among the most general of the constituents of plants are the vegetable acids, in which the elements of water with a certain excess of oxygen are combined with carbon[440]. In the fat oils and essential oils, in wax and the resins, again, the carbon is combined with the

[438] That these are deposited in the cells in a purely mechanical manner, is readily seen by the aid of the microscope. A delicate slice of a potatoe shows the starch granules lying within the cells; wetted with some strong tincture of iodine, the starch granules are immediately coloured of a beautiful violet blue, whilst the walls of the cells are tinged of a brownish yellow.

[439] The extrication of oxygen takes place under the influence of the sun's light; when fresh slips of plants covered with leaves are placed in water containing carbonic acid gas, this disappears; if they be now exposed to the light of the sun, they begin immediately to give off oxygen, which may be collected under a bell-glass and proved. Such a process of accumulation and decomposition of carbonic acid is repeated daily in the living vegetable: the roots and other parts which have the faculty of absorbing carbonic acid from the soil and air go on appropriating it continually; the gas accumulates in the body of the plant during the night and in cloudy weather, when some portion of it even passes off unchanged by the leaves; but in bright day-light, and particularly in sunshine, the carbon of the carbonic acid is assimilated by the solid parts of the vegetable, and the oxygen thus set free is given off.

[440] These vegetable acids are constituents of all vegetable juices, and exist very commonly combined with inorganic bases, so that they present themselves in the shape of neutral or super-salts.

elements of water alone, without any additional quantity of oxygen, or of this last substance there is present a very small proportion only, always less than the atomic weight in which oxygen combines with hydrogen; these substances consequently are compounds of carbon with the elements of water, plus a certain proportion of hydrogen. The hydrogen and oxygen of the substances mentioned, are undoubtedly derived from the absorbed water, which must be decomposed. Azote enters in but small proportion into the constitution of vegetables in general; still it is never wanting, and is a very principal element in vegetable albumen, in gluten or vegetable fibrine, and in legumen or vegetable casein, which are met with so invariably in the fruits and seeds of vegetables. Ammonia has very recently been indicated as the source of the azote present in vegetables and their products; this substance is always present in the atmosphere, although in very small quantity, and being precipitated in every shower of rain, is thus brought within the sphere of the absorbing and assimilating powers of plants[441]. Besides the four simple substances, of which the source, and the part they play in the nutrition of vegetables, have just been pointed out, vegetables generally contain certain inorganic substances,—alkalis, earths, salts. These are of course derived from the soil upon which vegetables grow, and seem quite indispensable to their health, and even to their existence. It is in the sap contained within the cells of vegetables that those remarkable combinations of elements, those formations and transformations of

[441] The important discovery that vegetables very generally aequire their azote from ammonia, is due to Licbig; up to his time it was always believed to be obtained directly from the atmosphere; but very few vegetables have the power of fixing the azote of the atmosphere; on the contrary, many actually give off azote, which they have taken up either by their roots or leaves from the atmosphere. Liebig has shown how and by what means ammonia is engendered and gets into the atmosphere for the use of vegetables. It is the product of the deeomposition of all animal and azotized substances, and is evolved in great abundance from putrifying eareasses, dunghills, &e. A certain proportion of the ammonia so engendered unites with aeids, and in the shape of a sulphate, a muriate, a nitrate, a phosphate, an oxalate, or a earbonate, is seized upon by the roots, and assimilated in the body of the vegetable; the carbonate of ammonia, again, as an extremely volatile salt, diffuses itself widely through the atmosphere, but it is brought down to the ground by the first shower of rain that falls, and so is made available to vegetation. It is on this account that rain-water and snow always contain ammonia.

proximate principles, take place which conduce to their ultimate nutrition, and to the preparation of their various secretions. The chemical processes as well as the vital processes are of a much more simple character in the bodies of plants than in those of animals, where a much greater variety of aliment of a much more complex composition is assumed, and where more diversified combinations of elements into new radicals, and transformations of these into the proximate principles of the various tissues and organs of the body, are effected. But the intimate or proper process of nutrition and secretion, or the specific influence of the organic substance upon the matters brought within the sphere of its chemical agency, is as much an enigma in the simplest vegetable as it is in the most complex animal.[442]

[442] [To me I own, that the Vegetable, in reference to the assimilating power, is more wonderful than the Animal. Vegetables *create*, animals seem only to *borrow*. Vegetables, by an inherent and wonderful virtue, decompound carbonic acid, water, and the salts of ammonia, and out of these fashion principles, as nearly as may be, identical with the most important proximate principles of the animal body. The process of assimilation may indeed be more simple, chemically considered, in the vegetable, but it is certainly more remarkable and of greater power than in the animal. Animals are entirely dependent upon vegetables; without the creating faculties of these, animals would speedily cease to exist. In connexion with the topics that immediately precede, M. Dumas' *Essai de statique chemique des etres organisês* (8vo. *Paris*, 1842, 2nd edit.) ought to be consulted. It is an admirable little work, and may be read again and again with renewed pleasure, clear in language, grasping and yet explicit in its general views. In some observations on the subject of this essay, which may be found in the 4th vol. of the 3rd series of the *Annales de Chimie* (1842), M. Dumas assigns the discovery of the important part which ammonia plays in vegetation to M. Schattenmann of Bouxwiller (1835); and the interesting fact that the azotized organic substances formed by vegetables pass without change into the bodies of animals, to Messrs. Prevost and Leroyer (1824). With all this there is still the great honour due to Liebig of having seen more clearly than any of his predecessors the bearing of the various data in the chemistry of vegetable and animal assimilation, which, up to the appearance of his two works already quoted, were in some sort disjecta membra. If Messrs. Prevost and Leroyer observed that vegetable albumen passed into the bodies of animals without change, they do not seem to have indicated vegetables as the creators of albumen and other azotized principles for the use of animals, which they certainly are. R. W.]

INTERCHANGE OF ELEMENTS.

§ 225. All organic bodies are in a perpetual state of renovation and decay; all are incessantly giving off and taking in the matters which enter into their constitution; there is no pause, no rest from the beginning of life to its end. The entire business of assimilation and secretion is in fact comprised in this ceaseless transformation of material; and the very existence of the organic vital processes may be said to depend on an interchange of external matters and elements, which, now portions of the vegetable, now portions of the animal kingdom, are soon restored by this again to recommence the round. What vegetables most require, especially for the development and maturation of their seeds and fruits, proceeds in great measure, as we have just seen (§ 224), from the animal body. The carbonic acid of the atmosphere is, in some considerable measure at least, derived from the bodies of men and animals, which expire and throw it off from their lungs and skin. This, vegetables greedily seize upon dissolved in water by means of their roots and leaves, turn the carbon into their proper substance, and give off the oxygen. Man and animals, again, inhale the oxygen so produced, and combining it with the carbon which they have taken into their bodies in the shape of aliment, restore it as carbonic acid gas. The azote of their food, again, they return in their excrements, their urine especially, as manure to the ground; and finally, by the decomposition of their bodies they give back all that remained with them when life ceased, in the shape of ammonia to that atmosphere whence vegetables by the aid of water mainly derive the supplies of azote that are necessary to their constitution and vital manifestations. The atmosphere in its ceaseless changes of temperature, and its unvarying sameness of elementary constitution, transports towards either pole the oxygen that is produced in such abundance by the vegetable world within the tropics, and in return bears back from the extreme north and south the azote evolved from the corrupting carcasses of sea and land animals for the uses of vegetation. Parallel with this interchange of elements on the grand scale is the constant interchange of elements which we observe in the individual. The change of matter

in the body of man is unquestionable in every one of the processes which subserve assimilation : it is obvious in reference to the fluids—the blood is renovated from the chyle, the chyle from the food; the blood in its turn is decomposed, or having supplied the elements of the organs, these are decompounded, and the products of the decomposition, the excretions, are rejected by the various emunctories of the body—the intestines, lungs, kidneys and skin. All the solid parts suffer changes in bulk, form, and structure. The evolution of the embryo, and the progressive stages obvious in the formation of its organs, the growth of the body in youth, the disappearance of the fat and the shrinking of the organs in old age, the various phenomena of resorption and regeneration, all bear testimony to the ceaseless change of matter in the body of the individual.

RETROSPECT.

§ 226. In the foregoing Book I have sought to lay before my reader a condensed account of the various phenomena which belong to nutrition and secretion. We have first analyzed the blood (Chap. I) as the source of all formation in the animal body, in its chemical and mechanical factors; we have then followed it in its outgoing and incoming channels (Chap. II), and have watched its primary formation in the embryo, and its regeneration by the solution and metamorphosis of the food in the digestive process (Chap. III). We have next seen how the blood is purified, giving off various compounds by means of respiration and excretion (Chaps. IV. and V.); some portion of the secreted matters being used again in certain processes of the economy. Finally, we have investigated the means by which the organism appropriates matters from without and changes them into its proper substance (Chap. VI). After contemplating the grand act of assimilation, we found ourselves at the point where the interchange of matter in the bodies of animals and of vegetables indicates the reciprocal influence of certain all-pervading physical and chemical powers, and we felt incited by the implanted desire for higher knowledge to view more closely the wonderful harmony of the alternating phenomena of which we obtained a partial glimpse, and to unravel the eternal laws which they obey. But here we are compelled to pause, and having examined the Generation and

development of the kind in the first Book, and in the one just concluded the organic-chemical processes connected with the bodily Maintenance of the Individual, we advance from the organic to the animal sphere, and enter on the investigation of the phenomena of Sensation and Motion, and their mechanical means and appliances. Having done this, we shall then find ourselves in a condition to take a survey of the vital phenomena as a whole, and in their several relations and mutual connexions, a subject which we regard as forming the proper matter of the GENERAL PHYSIOLOGY.

THE

SPECIAL HISTORY OF THE VITAL PROCESSES.

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OF SENSATION AND MOTION.

THE SUBJECT AND PLAN OF TREATMENT.

§ 227. The systems with which sensation and voluntary motion are associated, belong to the animal sphere of the organism. They are the media of reciprocal intercourse between our bodies and the external world, the instruments by which the existence and qualities of objects, and the great cosmic properties, light, heat, etc., are perceived. The organs which are efficient in this direction stand, farther, in a kind of peculiar relationship with that immaterial principle which we are bound to regard as distinct from any corporeal condition, but which, like all other phenomena in the created world, can only manifest its activity by the medium of material arrangements. The organs of sensation and motion, particularly those of the senses, are therefore to be viewed as a kind of outworks of the soul. As, however, it is a general law of the organised body, that no one part stands isolated from, and uninfluenced by, the others, but that all react reciprocally one upon another, so the nervous system, as the instrument of sensation and motion, is found to exert a peculiar influence upon the nutritive and reproductive processes, or the vegetative sphere of the organism, which it will be our business to study more closely by and by.

§ 228. We divide the processes of the animal sphere into four grand sections:—The first embraces the phenomena and laws of the nervous system in general, as well as of its particular peripheral parts. The second is devoted to the organs of sense. In the third the more intimate structure, the mechanism and organic activity of the organs of motion are investigated. The fourth treats of the central organs of sensation and motion.

SECTION THE FIRST.

STRUCTURE AND FUNCTIONS OF NERVES.

CHAPTER I.

MICROSCOPIC AND CHEMICAL ANALYSIS OF THE NERVOUS SUBSTANCE.

History of this Inquiry.

§ 229. There is no part of structural anatomy so difficult as that which has the brain and peripheral nerves for its object. Some portions of histology, it may fairly be said, had been occasionally more correctly seen by the older microscopical observers than by those of later times; but this is not the case as regards the nervous system[443]. It is only in the present day that something like a firm footing has been obtained here[444]. Still there has been no lack of

[443] The father of microscopical anatomy, Leeuwenhoeek, gave better figures than descriptions of what he saw; nevertheless as we meet with so mueh that is just in his narrations, we must infer that he actually knew the structure of the brain and nerves of sense better than a great number of those who came after him, such as Della Torre, Barba, Prochaska, &c. Fontana, again, gave better descriptions than figures, and was beyond all question well acquainted with the primitive fibres of the nerves. The first really good representation which I find of these, however, is contained in Treviranus's *Vermischte Schriften*, B. i. Tab. xiv.; where, nevertheless, the thing seen is incorrectly construed. See my *Beiträge zu Burdach's Physiologie*, B. v. S. 139. Bauer and Home, Prevost and Dumas, and Milne Edwards, were all misled by optical delusions, and describe the primitive nervous fibres as moniliform or beaded filaments. For the older literature see Hildebrandt's *Anatomy* by Weber, vol. i., and also Ehrenberg's work, quoted below, and Mandl's *Anatomie Microscopique*, liv. 2, Nerfs et Cerveau, Paris, 1838. Weber and Mandl have both given interesting contrasted views of the various older and more recent figures.

[444] The first who really broke new ground in this department was Ehrenberg, in his paper: *On a remarkable and hitherto unknown structure of the Brain in Man and Animals*, (*Beobachtung einer auffallenden, bisher unbekannten Structur des Seelenorgans bei Menschen und Thieren*, Berl. 1836,) in the Trans. of the Rl. Acad. of Berlin, and published separately, although he had given intimation

contradictory and erroneous observations in this any more than in almost every other department of minute anatomy[445]; and it is remarkable, that whilst the controversies of observers in other branches of histology have, for the most part, abated and tended to definitive conclusions, under the influence of mutual explanations and renewed inquiries, difference seems rather to have been upon the increase in the one which here engages us. Even now, indeed, and among men whose views and observations generally point to very similar conclusions, we have nothing like entire agreement in regard to the elementary anatomy of the nervous system[446]. Still a careful comparison of all that has been done leads us to discover a much more general accordance than at first

of his discovery so long ago as 1833 in Poggendorff's *Annalen*, B. xxxiii. Ehrenberg was the first who observed the tubular structure of the primitive fibrillæ in the brain and higher nerves of sense. The most important contribution of all to the minute anatomy of the nervous system, however, is that of Valentin: *On the course and termination of the Nerves (Ueber den Verlauf und die letzten Enden der Nerven,)* Acta Acad. Cæs.—Leop. vol. xxviii. p. 2. In this paper the subject is followed into every one of its most minute details, and with a precision which every day's additional experience makes us admire the more. Valentin observed the terminations of the nerves to consist of loopings of the primitive fibres; he conjectured a similar structure in the brain; he restricted the views of Ehrenberg in regard to the varicose structure of the primary fibres in the brain and nerves of sense, and first perceived the true character and connexions of the ganglionic globules, which had been figured by Ehrenberg as occurring in the invertebrata, speaking of them as a peculiar and important formation. Emmert *(On the mode in which Nerves terminate in Muscles. Ueber die Endigunsweise der Nerven in den Muskeln*, Bern, 1836,) and the younger Burdach *(Contributions to the Microscopical Anatomy of the Nerves. Beiträge zur mikroskop. Anat. d. Nerven*, Königsb. 1837) confirm the views of Valentin.

445 Among the number may be mentioned the incorrect views of Arnold, occasioned by optical deception *(Elements of Physiology*, Zurich, 1836), of Dutrochet; *(Mem. pour servir à l'Hist. des Animaux et des Vegetaux*, tom. ii. p. 475, &c.;) and of Berres (*in Med. Jahrb. d. Oesterr. Staates*, B. ix., and in the *Anat. d. Mikroskop. Gebilde*, Tab. iv.)

446 See the works, excellent in so many respects, of Remak: *Obs. anat. et micros. de system. nervosi structura*, Berol. 1838, of Purkinje and Rosenthal: *De formatione granulosa in Nervis aliisque partibus Organismi animalis*, Vratislav. 1839, and the plenary review of these writings by Valentin, in his *Repertorium for* 1840; as also his important paper in Müller's *Archiv* for 1839, which treats particularly of the structures described by Remak as organic fibres. The critical notices by Müller in his various Jahresberichten, as called forth by the different new works that appeared, deserve also to be consulted.

sight appears; and the very latest researches give us the comfortable assurance, that before long we shall have mastered the intimate structure of the central and peripheral parts of the nervous system[447].

Structure of the Primary Fibres of Nerves.

§ 230. Whoever would acquire a knowledge of the minute anatomy of the nervous system, had better begin by examining one of the peripheral nerves. Let a piece of one of the trunks or branches of a nerve, that can easily be dissected out, be chosen, and laid upon a glass plate: here let the nervous bundles be separated or teazed out by the aid of a needle in either hand, until free spaces of the glass plate appear; let the preparation now have a drop of serum or of albumen added to it, and then be covered with a piece of thin glass[448]. Under a magnifying power of from three to four hundred diameters, numbers of transparent cylindrical, straight, or slightly sinuous filaments will be perceived as the chief structure, having a mean diameter of from $\frac{1}{200}$th to $\frac{1}{300}$th of a line, and always proceeding distinct from one another, never anastomosing. These are the PRIMITIVE FIBRES of the nerve (figs. CCXXI. *et seq.*) If these fibres have undergone little or no change, each is severally seen to be bounded by a double contour, an appearance which must be viewed as the optical expression of a transparent covering or membrane. The middle space is completely transparent. When the nerve has suffered change from pressure, imbibition of water, or the like, the appearance is altered. In the middle clear space granular or grumous particles or masses are perceived, which, under pressure, escape from the divided ends

[447] Vide in particular, the newest and best short observations resting on individual observation by Gerber, in his *General Anatomy*, Bern, 1840, Anglice, with Additions by G. Gulliver, London, 1841; also Krause's *Manual of Human Anatomy*, (German,) and Bruns' *Elements of General Anatomy*, (German,) Brunswick, 1841.

[448] The nervous substance, particularly of the central parts, undergoes change with the greatest rapidity. It is therefore necessary to examine it when quite recent—to procure the nerves of amputated limbs, or of animals just killed, &c., and to avoid water and pressure as much as possible. Even serum and albumen are not altogether without influence. For covering, there is nothing so good as the extremely thin glass plate which Oberhäuser, of Paris, supplies for this purpose.

of the primitive fibres. (Fig. CCXXI., A, to the right.) Other changes, but more difficult of apprehension, also take place in the lateral contours of the fibres, which are made up of the double lines. (Fig. CCXXV., A, one of the primitive fibres is altered.)

To observe the primitive fibres of nerves in their normal situation, the best subject is the delicate flat muscle of some small animal,—one of the muscles of the eye of the common sparrow, for example (Fig. CCXXII.),—which must be gently pressed be-

Fig. CCXXI.

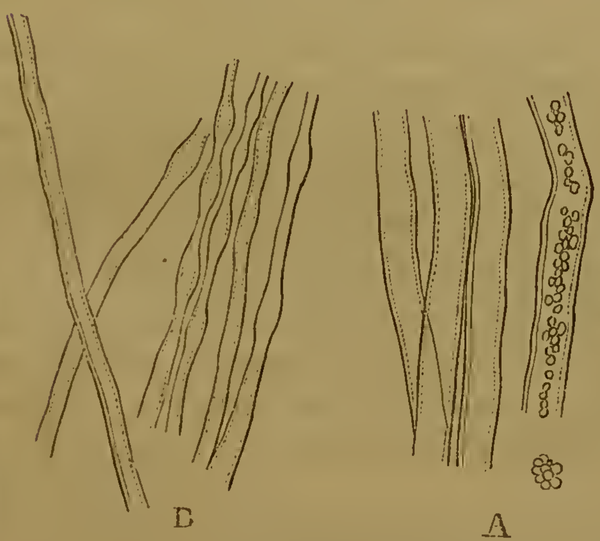

Fig. CCXXI.—*A*, Primary fibres of a human nerve. *B*, primary fibres (more highly magnified) of the brain.

Fig. CCXXII.

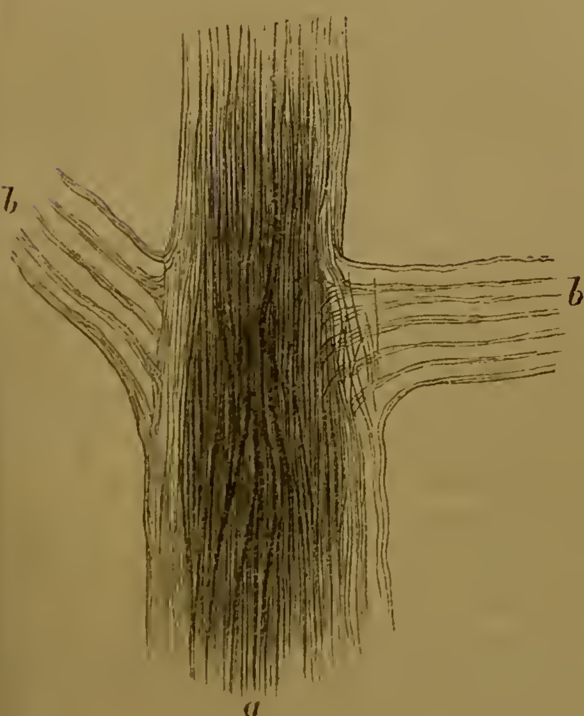

Fig. CCXXII.—Branch of a nerve distributed to one of the muscles of the eye of a sparrow.

tween two plates of glass. Here, in the middle trunk (*a*), which to the naked eye looked finely fasciculated only, a great number of primitive fibrils are perceived lying over one another, but without running altogether parallel, inasmuch as some diverge a little to the right, others a little to the left, some proceed from below upwards, others from above downwards, but all preserve the main course onwards. They lie so close, and cover each other so much, that their structure individually cannot be distinctly made out. At the parts where smaller branches are sent off transversely, however (Fig. CCXXII., *b*, *b*), the structure of the primary fibres running in a parallel direction may be seen as distinctly as when they are separated by art. It frequently happens that we may tear fresh primitive fibres in such a way that the broader, clear, middle portion alone retains its continuity, the bounding lines having given way transversely; the middle portion is then seen to be inclosed within an extremely delicate contour. From all this, it may be inferred that each primitive fibre consists of a very clear included substance, and a transparent tubular sheath. The double line or contour of either side being the optical expression of the inner and outer wall of this tube[449]. Other observers admit a more compound structure[450]; and some have

[449] In many instances, when perfectly recent nerves are examined in their natural situations, these double contours are not visible, and it then appears as if the primitive fibrils consisted of a homogeneous substance. I have particularly observed the auditory nerves in this way.

[450] On the different views of this matter, see Bruns *Op. Cit.*, p. 143, and Köstlin's *Microscopical Inquiries in reference to Human Physiology* (*Die mikroskopischen Forschungen im Gebiete der mensch. Physiologie*), Stuttg. 1840, p. 7. Others, among the number Valentin (Sömmerring's *Anat.*, new ed., vol. iv., p. 4.), have lately distinguished three parts in the peripheral primary nervous fibre, examined in the most recent state: 1st, an outer sheath of cellular tissue—vagina externa s. cellulosa, composed of filaments of cellular tissue, lying close together, and running, for the major part, lengthwise along the primitive nervous fibres; this tunic is apt to become detached in the process of isolating the primitive fibres, and so to escape observation. 2d, A bounding or true containing or inner sheath—vagina interna, a highly delicate membrane, surrounding the nervous contents immediately, which generally appears entirely homogeneous; but which under favourable circumstances, with a good instrument, shading and lamp-light, is perceived to be composed of fibres. The appearance is as if two spiral formations, crossing one another, were wound about the tube. 3d, The nervous contents—contenti nervorum s. fibrarum nervosarum, which, examined when perfectly fresh, appear homogeneous, and more or less opalescent or milky, and

even spoken of a ciliary epithelium lining the inner aspect of the sheath[451].

§ 231. These primary tubes or fibres of the peripheral nerves are similar, with very slight modifications, in every part of the nervous system. It is necessary, however, to except from this general rule the first and second cerebral nerves[452]. In the auditory nerve the fibres are somewhat more delicate than elsewhere.[453] They also very commonly appear rather finer than wont where they traverse ganglions. They appear to be distributed over the periphery of the body, without in any instance anastomosing. They have a central and a peripheral termination. With reference to the first,

with sharp edges, not differing in any way from the rest of the contents. This contained nervous matter is extremely liable to undergo change spontaneously after death, and is powerfully affected by re-agents. It becomes turbid, thick, and coagulates, and then presents granulations and granular masses, having lost its transparency and homogeneous character—coagulatio contenti nervorum. Bruns views the outer bounding line as the optical expression of an extremely thin, transparent sheath; whilst I, with Ehrenberg, regard the inner more delicate bounding line as expressive of the internal wall of the somewhat thick primitive tubulus. That the envelopes are composed in the way Valentin describes them, I have never been able to make out with any kind of certainty. Krause (l. c., p. 50,) gives an account of the structures in question, which agrees in all respects with my observations.

[451] Remak is the first who speaks of a ciliary movement within the primary nervous fibrils (l. c., p. 32). Gerber also informs us that he had observed a motion of the same kind (*General Anatomy*), and gives a rude figure of a ciliary structure as he saw it. According to Valentin, such a motion, which perchance indicates the presence of a ciliary epithelium, may be perceived, in particular instances, on the inner surface of the bounding membrane or sheath of isolated, still warm primitive fibres, but only by lamp-light. Valentin himself speaks of the appearance as extremely doubtful, scarcely to be judged by the microscope in its present state, and certainly not to be made the basis of any kind of speculation or inference. These views and doubts have my entire approbation. I have even given a kind of particular attention to the point; but with instruments of all kinds, and a power of 1200 diameters, which still gave distinct images, aided by the apparatus of Dujardin, I have been able to perceive nothing of the kind, saving and excepting always that well-known optical glistening, which may be produced at any time.

[452] The primary fibres of the olfactory and optic nerves bear the strongest analogy to those of the brain, as Ehrenberg first showed: they are among the very finest.

[453] In the auditory nerve the primary fibres are much thicker than in the olfactory and optic nerves, and in their structure approximate more to the peripheral nerves at large: their sheaths, however, are more delicate.

or where they enter the brain or spinal cord as roots of nerves, they pass immediately into the white medullary fibres, or central parts, and at the same time become by one half, or even two thirds, smaller. The primary fibres of the brain and spinal marrow, as well as those of the olfactory and auditory nerves, are in some cases so delicate, that they measure but the $\frac{1}{1000}$th of a line in diameter: frequently, however, they are thicker, from the $\frac{1}{400}$th to the $\frac{1}{500}$th of a line in diameter. These fibrils, of different dimensions, are constantly observed running over, and under, and near to one another. (Fig. CCXXI., B, CCXXII., and CCXXIII., C.) Examined in the most recent state possible, they are, for the major part, cylindrical, but in part also knotty or varicose, inasmuch as they exhibit little oval or rounded enlargements in their course. (Fig. CCXXI., B, CCXXIII., A, B.) It is doubtful whether or not this varicose state is accidental only, or is really peculiar to certain primary fibres in the living state[454]. So much is certain, that the knots are constantly seen arising under the eye of the observer, and that they are frequently

[454] Ehrenberg regarded this varicose structure as characteristic, and peculiar to the fibres in question. The opinion that the primary fibres of both the brain and spinal cord are naturally cylindrical, appears to be more and more on the increase of late.

Fig. CCXXIII.

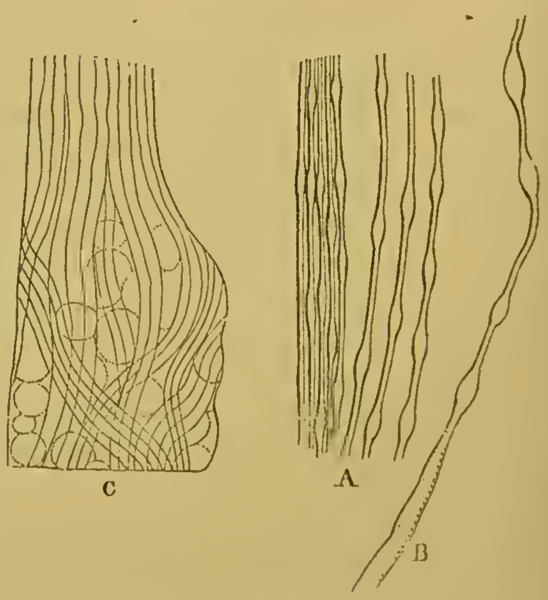

Fig. CCXXIII,—*A*, primary fibres of the olfactory nerve of man. *B*, A primary fibre from the thoracic portion of the spinal chord of man. *C*, A thin slice from the outer aspect of the ophthalmic ganglion of man. After Valentin.

effects of the methods of investigation pursued[455]. There is nevertheless this peculiarity to be noted, in regard to the primary fibres of the central parts, that they are much more apt to assume the varicose condition than those of the periphery; a peculiarity that seems to be connected with their structure. The sheaths, in fact, of the central primary fibres are much more delicate, although in general still characterised by the double contour, than those of the peripheral fibres. In the central fibres, too, the sheath and contents appear to be far more intimately connected; in many cases they are completely inseparable, so that the contrast as betwixt sheath and contents disappears[456]. These delicate primary fibrils of the central masses run in such variety of ways, crossing and interlacing, and forming such a tangled skein, that it is impossible to follow them to the roots of the nerves, or towards the periphery of the brain and cord, and so to make certain that they never anastomose. To all appearance, however, they never divide; and they seem no more to run into one another, or to communicate by anastomoses here, than they do in the peripheral parts of the body. But these fine primary fibres of the central parts enlarge conspicuously and immediately at the entrances of the different nerves into the brain and spinal cord.

Termination of the Primary Fibres.

§ 232. A very important question, which naturally presents itself in connexion with the primary fibrils, is this: how do they

[455] The varicose state is caused most certainly by the imbibition of water. The part in which the medullary substance and lamellæ of primary fibres can be most advantageously examined, I find to be the valvula cerebelli of a small animal, such as a rabbit or a bird. This part is removed, and, being laid smooth upon a plate of glass, is gently compressed. E. H. Weber demonstrates the primary cylinders in this way: he covers a small piece of the cerebral substance with albumen; and then, with a couple of fine needles, bent at the point, he puts the fibrillæ on the stretch.

[456] So it seems to me, although the greater number of observers, among the number Remak, very lately in Müller's *Archiv*, (1841, S. 512,) maintain that the primary tubules in every part of the nervous system are alike in structure, and consist of the above-named three elements: the pale sheath, (a kind of remainder of cellular tissue,) the thick dark medullary sheath, and the pale central fibre. Bruns also disputes the presence of any special cellular sheath in the central parts of the nervous system.

end?—Although generally traced with difficulty, the peripheral terminations of the nervous fibrils are still much more easily demonstrated than those of the centres. United into bundles, and surrounded with cellulo-membranous sheaths, (Neurilema,) the primary fibres penetrate all the organs nearly to their peripheral confines, to where they are covered with epithelial or epidermic formations. Here it is that the bundles of primary fibres separate and form plexuses—*terminal plexuses*, as they have been designated; at last single primary fibres form loops, or rather, two primary fibres meet and form a loop,—*terminal loops*[457]. These loops are smaller or larger in different tissues. (Fig. CCXXIV., CCXXV.)

[457] Valentin gave many very good representations in his paper already quoted in the *Nova Acta Acad. Natur. Curios.* Prevost and Dumas speak of loop-like terminations of the nerves. They were clearly demonstrated by

FIG. CCXXIV.

FIG. CCXXIV.—A small portion of the terminal plexus of primary fibres of the auditory nerve in the auditory sac of the Pike (Esox lucius).

Wherever the primary fibres of nerves have been distinctly traced to their extremities, this mode of termination in loops has been observed, so that it appears to be general, and even to extend to the nerves of special sense, with the single exception of the olfactory and optic nerves, in the peripheral expansions of which, no loopings have been positively ascertained to exist, although no one has yet condescended upon any other mode of termination in regard to these two nerves[458]. I have already said that the mode of termination of the primary fibres was much more difficult of demonstration in the central parts than in the peripheries. (Fig.

Valentin, Emmert, Burdach, Gerber, and others, in the museles, the skin, and other tissues. Whcrever I have been able to see things clearly, I have diseovered these loop-like terminations. The ear is the best subject for commcneing the study of the looped-terminations of thc nerves; the ampullæ of vertebrate animals at large, partieularly of fishes, are excellent subjeets.

[458] Valentin will also have it that he had seen looped-terminations of the primary fibres in the retina; this author's observations, however, have not been eonfirmed; I have never myself sueeecded in seeing anything of the kind; and I am even sceptical in regard to the enlargements in the nervous papillæ. See what is said further upon this point, under the head of the Organs of Sense.

Fig. CCXXV.

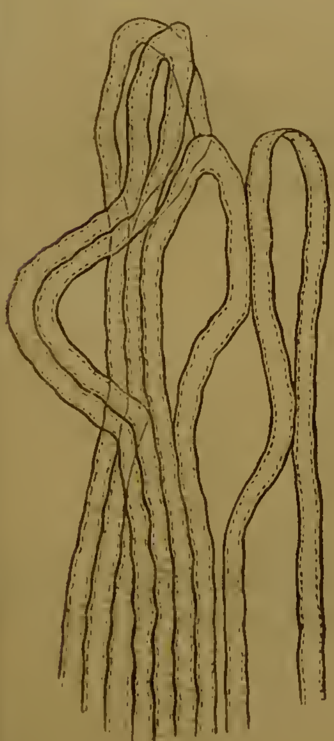

Fig. CCXXV.—Terminal primary fibres from the eiliary ligament of the common Duek. After Valentin.

CCXXVI.) It is impossible at present to say positively that they again turn round loop-wise, on the surface of the brain, as certain observations would lead us to conclude that they did[459]. [In ganglions, the primary fibres separate and become interlaced and convoluted, but apparently without terminating; they by and by resume their onward course. (Fig. CCXXVII.) Do not a certain

[459] Valentin recognises loop-like terminations in the periphery of the brain, and gives a figure of the arrangement as he saw it. (l. c.) With every endeavour, I have never succeeded in obtaining perfect conviction of this interesting fact in minute anatomy, although, in examining the corpora quadrigemina of the pigeon, I have several times thought that I could perceive the primary fibres lying in loops among the ganglionic cells. According to Remak's latest observations, the hemispheres of the brain in man are covered by an extremely delicate layer of white substance, consisting of primary fibres, which run horizontally on the superficies of the convolutions, and cross each other in every direction. Remak could not determine that they penetrated perpendicularly into the gray substance, or how and in what way they were connected with its elements. Müller's *Archiv*, f. 1841, S. 508. [Dr. J. Hughes Bennett on one

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Fig. CCXXVI.

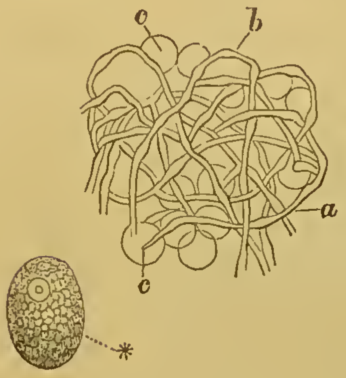

Fig. CCXXVI.—Central terminal fibres from the yellow substance of the cerebellum of the common pigeon: *a*, terminal plexus of primary fibres; *b*, loopings of the terminal fibres; *c*, ganglionic globules *. A ganglionic cell from the Gasserian ganglion of man, removed from its sheath and highly magnified.

Fig. CCXXVII.

Fig. CCXXVII.—Second abdominal ganglion of the sympathetic nerve of the Fringilla spinus, to show the course of the primary fibres.

number of fibres take their origin in the ganglions, in the same way as they do in the brain and spinal cord? The bundle that quits the ganglion is often manifestly larger than that which enters it. R. W.]

Ganglionic Corpuscles, Ganglionic Cells.

§ 233. Besides the tubular or primary fibrous formations now described, there is a second and general elementary structure in the nervous system, entitled the *ganglionic, or nervous globules,* better the *ganglionic cells or corpuscles.*[460]. These corpuscles are met with in the brain, spinal cord, and ganglia, and also here and there in particular nerves. The cineritious, or gray nervous substance, wherever it occurs, be it deep-seated or superficial, consists of aggregations of these ganglionic corpuscles. They have always a certain quantity, more or less, of the tubular or primary fibrous structure mixed with them; the more abundant the primary fibres, the lighter is the mass; the fewer they are, the darker is its colour. The ganglionic corpuscles, particularly in the brain and spinal cord, are much more delicate and easily destroyed than the primary fibres. To study them, it is well to begin with the Gasserian ganglion of a small animal, such as a rabbit, or a thoracic ganglion

occasion observed the cerebellum crossed in different directions by delicate white lines, resembling the minute branches of a nerve. These were, of course, much too large for primary fibres; they were distinctly visible to the naked eye; it would have been interesting had they been found by the microscope to consist of bundles of nervous fibres. R. W.]

[460] We are indebted to very recent times for the discovery of these remarkable structures; Ehrenberg, indeed, observed and figured them; but Valentin has the honour of having first pointed them out as a peculiar and essential element in the nervous substance. He first named them nervous, or nerve-corpuscles,—corpuscula nervea, and globuli nervosi nucleati; and in his latest work (Söemmerring, p. 8, *et seq.*) he arranges them into two principal groups: nervous corpuscles of the peripheral nervous system,—ganglionic corpuscles or globules, and nervous corpuscles of the central parts—central nucleated globules. [Gall and Spurzheim did not use the microscope; but that they were perfectly well aware of the high importance of the cineritious or gray matter, which is made up of ganglionic cells, appears from the name they gave it—matrix of the nerves. They, in fact, saw it as the essential element, as the source of power, in the nervous system, and regarded the white fibres as mere conductors. See their *Recherches sur le Système Nerveux, &c.; Mémoire présenté à l'Institut le* 14 *Mars*, 1808. R. W.]

of a small bird (Fig. CCXXVIII., B,*; CCXXIX., *a*)[461]. Here, they mostly appear as globular or oval, indistinctly granular bodies,

[461] Great care is generally requisite in proceeding to study the ganglionic corpuscles. It frequently happens, however, that we get an excellent view of these corpuscles in their natural position, by examining a small ganglion under gentle compression (Figs. CCXXVIII., B; CCXXIX., A); here, they appear surrounded by, or intermixed with, primary fibres running or forming a plexus

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Fig. CCXXVIII.

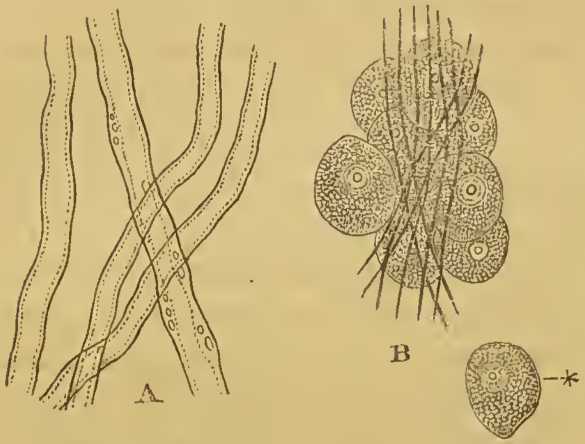


Fig. CCXXVIII.—A, Single primary fibres from an intercostal nerve of the common sparrow. B, Several primary fibres and ganglionic cells, from one of the thoracic ganglions of the same bird.* A single ganglionic cell, with a clear nucleus and darker nucleolus.

Fig. CCXXIX.

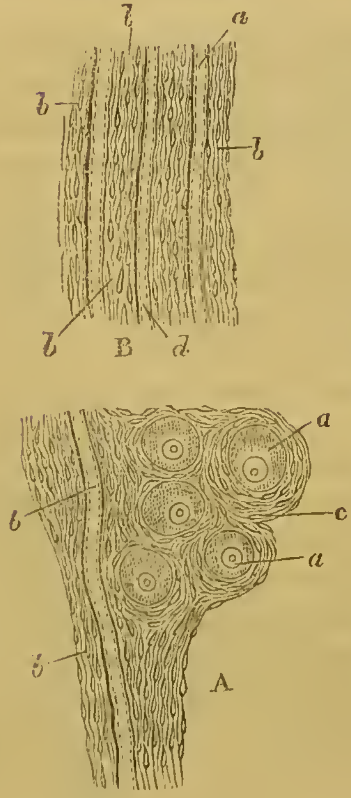


Fig. CCXXIX.—A, Thin slice from the superior cervical ganglion of the calf: *a*, ganglionic globules; *b*, primitive fibre; *c*, involucrum of the ganglionic cells. B, Thin slice from the soft nerve of the plexus maximus carotidis of the calf; *a*, *a*, *a*, isolated primary fibres; *b*, *b*, thick sheaths of the same. After Valentin.

having internally a clear vesicular-looking nucleus, which in its turn mostly includes a nucleolus[462]. They are composed of extremely fine molecules, connected together by a semi-fluid, glutinous, or viscid, amorphous substance. It is doubtful whether or not they possess a delicate transparent proper capsule. For the major part, however, each ganglionic corpuscle is surrounded by a cellulo-membranous capsule or sheath: extremely delicate, grayish or reddish coloured cellulo-membranous fibres, furnished with nuclei, are interwoven into true capsules; but from these the ganglionic corpuscles very readily become detached and fall out. Frequently, as for instance in the cervical portion of the sympathetic nerve, (Fig. CCXXIX., A, and B,) this cellulo-membranous sheath is so highly developed, that the ganglionic corpuscles (A, *a*, *a*), appear to be bedded in a kind of matrix, which is only intersected here and there by single primary fibres (B, *a*, *a*); these, like the corpuscles, seeming to be separated and kept apart by the abundant cellular tissue. This cellular tissue, with its nucleated fibres, has been erroneously described as a third and distinct special element of the nervous system, under the name of the *organic fibrils*, probably from their abundance in the sympathetic and its ganglia, or of the nodulated fibrils—fibrillæ nodulosæ[463].

The ganglionic corpuscles present numerous varieties in regard to form, size, arrangement, and the structure of their remoter elements. They are singularly delicate and destructible in the central masses.

among them (CCXXVIII.) By tearing such a ganglion with a couple of needles, it is easy to detach the corpuscles from their nidus, and to get a view of them isolatedly.

[462] The clear nuclei and nuclear corpuscles, or nucleoli, are extremely minute, and even appear relatively somewhat too large in Fig. CCXXVIII. The ganglionic corpuscles themselves, are of very different dimensions,—from the $\frac{1}{100}$th to the $\frac{1}{50}$th of a line in diameter; the nuclei from the $\frac{1}{300}$th to the $\frac{1}{200}$th of a line.

[463] The indication of these fibrils of the cellular tissue as organic nervous fibres, as a peculiar system, running parallel with the sensitive and motory fibres, and connected with the vegetative functions, originated with Remak; (*Obs. Anat.*, 1838,) Müller adopted his views, and Krause described the fibrils in question under the title of *Knötchenfibrillen*—nodular fibrils. Valentin combated this notion in his excellent criticism of Remak's work in Müller's *Archiv*, f. 1839, S. 139, and in his own *Repertorium*, B. iii., S. 76., B. v., S. 79. So also did Bruns (*Op. Cit.*, p. 149). I need not say that I agree with them entirely.

Here, the cellular sheath, just described, is entirely wanting; and the finely granular substance of which they consist, and the clear nucleus which they contain, are so diffluent, that it is seldom we succeed in finding more under our microscopes than a homogeneous, finely granular mass. Whether from the great nervous centres, or from the more peripheral ganglia, they are generally either round or oval in figure (Figs. CCXXVI., CCXXVIII.$_*$; CCXXIX., *a*, and CCXXX., *a*); frequently, however, they are elongated, sausage-shaped, four-cornered, tetrahedral, and furnished with off-sets or processes (Fig. CCXXX., B); it is seldom that two are seen connected by a bridge. The nucleus is always clear, roundish, or lengthened and simple; the nucleolus is extremely small [464]. In their general external appearance, these ganglionic corpuscles have a surprising resemblance to primitive ova; they are constituted after the general type of cellular formations, although they have more of the character of solid bodies, than of true cells with fluid contents.

§ 234. The cellular tissue serves at once as the bond of union, and means of separation, of the individual elements of the nervous system. It occurs in variable proportions as the insulator of the primary fibrils and ganglionic corpuscles, and at the same time

[464] Remak and Valentin occasionally saw two nuclei in a single corpuscle; more rarely they observed two corpuscles united by a commissure. I have never myself met with either of these arrangements.

Fig. CCXXX.

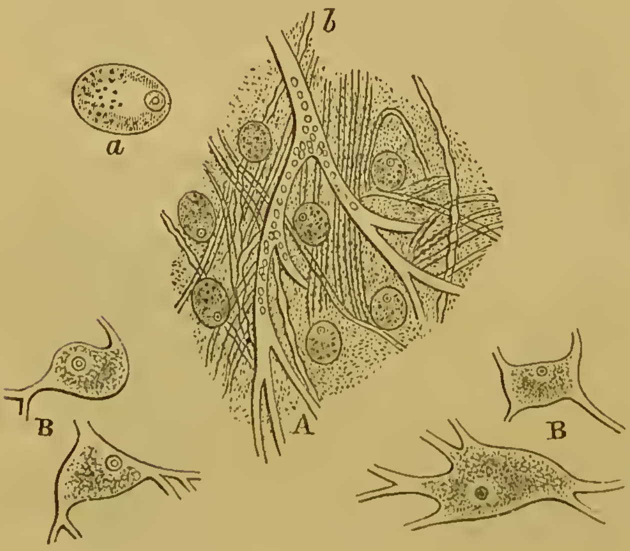


Fig. CCXXX. — Primary fibres and ganglionic globules from the human brain. A, Ganglionic globules in the substance of the thalamus, mixed with varicose primary fibres. *a*, A single ganglionic globule or cell, highly magnified; *b*, A blood-vessel. B, B, ganglionic globules with processes of various form, as they are met with in the black substance of the crura cerebri. After Valentin.

supplies a bed for the blood-vessels, the capillary subdivisions of which are always found playing about these fibrils and bodies, in large numbers, and presenting a distribution very much akin to that which has already been spoken of as occurring in glands. (§ 198). It happens not unfrequently, that pigmentary deposits take place in the walls of the ganglionic corpuscles, which then present the deep colour that characterizes several of the ganglia.

Chemical Composition of the Nervous Substance.

§ 235. This is a subject of very subordinate consequence, and, in fact, affords us no footing whatsoever in our investigation of the functions of the nervous system. The chief constituents of the brain and spinal cord are albumen and a variety of phosphoriferous fats, of which, besides cholesterine, four different kinds have been specified by the latest inquirers. Besides these, the brain is very rich in water (it contains about 80 per cent.); in its physical composition, it may be said to bear a stronger resemblance to an emulsion, than to aught else[465].

CHAPTER II.

GENERAL PHYSICAL PROPERTIES OF THE NERVES.

Of the active principle in the Nerves.

§ 236. Of the peculiar potential or active element in the nervous system, we know nothing. The subject, however, is altogether indifferent to us, and we only allude to it, for the sake of securing it a determinate name and expression. We shall go on to speak of this unknown element under the title of the NERVOUS AGENT. Some short time ago, physiologists seemed very commonly to agree

[465] The elaborate analysis of Berzelius (*Chimie*, 4th ed.) may be consulted. The first somewhat complete analysis was made by Vauquelin. He found that the brain consisted of uncoagulated albumen, and two kinds of fat, one fluid, the other solid, but both containing phosphorus. Couerbe described the different species of cerebral fat more particularly; they consist, according to him, of Cholesterine, Cerebrote, Eleencephalote, Cephalote, and Stearoconote. These conclusions of Couerbe have, however, been called in question by several chemists, particularly Wöhler, who declares them untenable.

in considering this agent as one and the same with electricity, and this notion has even very lately been again brought upon the scene[466]. Such an idea, however, can be demonstrated most satisfactorily by experiment, to be without all foundation: the nerves are conductors of electricity, in common with every other moist animal substance, but not more so, and not less. For our own part, we view the nervous agent as a peculiar and primary animal phenomenon, as an activity *sui generis.* Whether or not it be a dynamic principle, or force, as some conceive, and then go on to speak of it as the nervous force, or a delicate material element, one of the same category as the imponderables light, heat, electricity, magnetism, is unknown[467]. Happily it is matter of indifference, which view be espoused in analysing the phenomena with which alone we have to do in this place; just as it was long of no moment, in scrutinizing the phenomena and laws of optics, whether the theory of emanations or of undulations was adopted. Even as little do the manifestations of the soul stand in any immediate connexion with the nervous agent[468].

General Functions of the Nerves.

§ 237. The central parts of the nervous system are the brain and spinal cord, and these are at the same time the centre of the

[466] The identity of the nervous agent and electricity had not been seriously maintained by any one for a great many years, which makes the recent advocacy of this idea by Faraday the more singular. He holds that the nervous power is not merely analogous in a certain degree to such powers as heat, electricity, and magnetism—which might be granted in various respects—but that it is an inorganic force, although "he has not yet been able to satisfy himself by facts that the nervous fluid is merely electricity."—See his paper, interesting in so many respects, *On the electrical Eel*, in the *Philos. Trans.*, 1839, pt. 1. [The late John Abernethy was the great advocate, among ourselves, for the identity of the nervous power and electricity; and such influence had he, that at one time it was even dangerous to oppose or deny the doctrine; he who did so, being looked on as a scoffer and impious person. R. W.]

[467] I have here purposely avoided the expression *nervous fluid*, to escape the dilemma of appearing to give any countenance to the entirely hypothetical notion of a kind of nervous fluid circulating in the primary fibrils, which seemed for a time to receive support from the presumption of ciliary motions occurring in these structures, a presumption, however, which we have seen to be entirely unsupported by facts.

[468] On the subject of the distinction between the soul and the nervous

nervous agency, and the seat of all the sensorial and spiritual manifestations. The nerves are conducting organs, which bring the brain into communication with all the parts of the body. The sum of the primary fibres which are contained in the whole of the nerves, proceed from the brain and spinal cord, and return through the peripheral loopings to the spinal cord and brain again. The spinal cord, as we shall see by and by, is at once a central and conducting organ. In the nervous system at large, there is a double or two-fold conduction or current of the nervous agency: 1*st*, From the peripheral organs to the brain. This conduction is effected by peculiar primary fibres, which have been designated by the title of SENSITIVE FIBRES, or FIBRES OF SENSATION; they transplant, as it were, an impression which they have received at their peripheral ends to the brain, and here excite the idea or consciousness of the impression. They are, therefore, the mediate instruments of sensation. The sensitive fibres contained in the cerebral nerves enter the brain immediately through the roots of these nerves; the sensitive fibres contained in the spinal nerves, again, collect into the posterior roots of these nerves, and proceed in the posterior strand of the spinal cord, to the medulla oblongata. 2*d*, The conduction proceeds from the centre to the periphery, and this is effected by the MOTORY FIBRES. These go to the muscles, are conductors of the will, and are connected with motion in general. They collect in the anterior strands of the spinal cord, and from this part proceed in the anterior roots of the spinal nerves.

The fibres which constitute the ganglionic system, or great sympathetic, have been viewed as a third kind of nervous fibres. These form a peculiar system, abstracted in very great part from the influence of the cerebro-spinal system, and serve as conductors to the organs of the chylopoesis and generation of the nervous agency which is necessary to them for the manifestation of their appropriate functions. Careful consideration of all the phenomena presented, however, has shown, that in the sympathetic nerves there are fibres of sensation as well as of motion, and that these, as in the case of all the other nervous fibres, issue from and enter the brain.

power, see the attractive essay of Schroeder van der Kolk, *On the difference betwixt Inanimate Natural Force, Vital Force, and the Soul*, (*Ueber den Unterschied zwischen todten Natur-Kräften, Lebenskräften und Seele*, Bonn, 1836); see also the *general Physiology*.

The sensations and motions with which the ganglionic system is connected, only suffer certain modifications, which will be investigated more particularly in the sequel.

Hitherto, no obvious anatomical difference has been detected between the fibres of sensation and those of motion; the difference that certainly exists is recognised solely on the grounds of experience.

§ 238. In particular nerves, perhaps in all nerves, with the exception of those of the special senses, sensitive and motory fibres are present, intimately mingled with one another. The several nerves and their branches are therefore to be viewed as collections of primary fibres, having different functions, proceeding together to the organs to which they are destined respectively. Microscopic examination farther shows us that the several primary fibres always remain separate from one another, never blending or anastomosing, each keeping its course distinct from all the rest from the brain to the remotest part of the body. Whether in the periphery of the body fibres of the same or of different functions unite to form loops or not, is unknown. In all likelihood, however, fibres of like office alone compose peripheral loops.[469]. As we have just seen, the course of the nervous agency in the nerves of sensation is centripetal, in the nerves of motion, centrifugal. It is, therefore, and on this account, that the impression which a nerve of sensation receives in the periphery, is only perceived when it is in uninterrupted communication with the brain and spinal cord. Stimuli of all kinds excite sensations in this way. Applied to motory or muscular nerves, the same stimuli occasion contractions in the muscles to which the nerves are distributed. The effect

[469] The anatomical fact, that the primary fibres form loops at the periphery, has hitherto afforded no secure grounds for conclusions in regard to their functions. Here, unhappily, we find ourselves in the maze of hypothesis. According to Carus, the conduction in these loops or anastomoses of an outgoing and incoming fibre, takes place in the sense of the circulation: a motory fibre having attained the periphery, passes into a sensitive fibre. Vide Müller's *Archiv*, f. 1839, S. 366, and f. 1840, S. 521. What renders it most probable that sensitive fibres only, and motory fibres only, combine to form loops, is the fact that such is obviously the arrangement with the fibres of the auditory nerve. (Vide § 232). It is easy enough also to observe loopings in the skin and in the muscles, and we might infer that here nerves of sensation only, there nerves of motion only, anastomosed, were it not that the skin possessed a certain contractility dependent on the nervous system (goose-skin); and the muscles a sensation, which is often very decided, as in cramp.

follows in both instances, whether the nerve that is stimulated be in uninterrupted communication with the brain and spinal cord, or be cut off from its connexion with the nervous centres. Of course, however, the nerve must remain in uninterrupted communication with the part to which it is distributed.

Regeneration of Nerve.

§ 239. By the division of a nerve, as we have seen, the transmission of the nervous influence in the determinate direction is interrupted. If a mixed nerve is cut through, impressions made on those parts that are supplied by the nerve below the division are not transmitted to the centres, and the will reaches not beyond the point at which the solution of continuity exists. But let the divided nerve grow together again, and the original capacity of conveying impressions and volition is recovered, and a microscopical examination of the cicatrix shows, that in the mass which the exudation has formed in the first instance, new primary nervous fibres are actually produced, precisely similar in every respect to the original ones. The only observable differences are, that the newly engendered fibres are not present in such numbers as in normal nerve, that they seem more confusedly mingled together, and that they are separated to a greater extent by newly formed cellular tissue, and other exudative matters. These peculiarities suffice to account for the less perfection of function which we observe along with a reunited nerve, neither sensation nor motion being usually recovered completely under such circumstances. The time required by a divided nerve for the recovery of its functions, is subject to great variations[470].

[470] Steinrück, in his inaugural dissertation: *De Nervorum Regeneratione*, (Berol. 1838, c. Tab.) gives a very good summary of all the known facts upon these topics, and in addition numerous original experiments. Vide also the excellent researches of Nasse (Müller, *Archiv.*, 1839, S. 495,) and of Günther and Schön (*Ib.* 1840, S. 270). Hitherto, the event following the division of nerves is only known in reference to those of peripheral parts. The time in which the union and regeneration of a nerve are accomplished is various, sometimes it is a month, sometimes it is more. Similar cicatrizations must take place in the central organs, as is made obvious by what happens in cases of apoplexy, and injury of the brain and spinal cord, cases in which the functions are often recovered at a very late period and very gradually. In the nerves of the special senses, regeneration is never else than incomplete, and the function seems not to be recovered. Vide § 246, Annot 1.

Irritability of Nerves.

§ 240. It is of the greatest importance to examine into the irritability of the nerves, and to ascertain the nature of the different stimuli which they obey. It is by the medium of an accurate knowledge of such relations, indeed, that it becomes possible to discover the functions of each individual part of the nervous system, to undertake an extensive series of empirical experiments, which should supply a sure basis for a physiology of the nervous system. Stimuli or irritants are of different kinds, but may all be arranged under the five following general heads: 1*st*, MECHANICAL STIMULI. To this chapter belong pressure, blows, pricking, wounding, and separation of the primary fibres. By all these influences sensation is aroused, and when they are excessive, and a cutaneous nerve is implicated, pain is produced. The nerves of the special senses, however, when mechanically stimulated, do not excite ideas of pain, but perceptions more or less in accordance with their peculiar functions:—pressure on the retina causes sensations of light; a blow on the head, riding in a rough carriage, etc., when the auditory nerve is mechanically shaken, is followed by humming or ringing noises in the ear. We have a familiar illustration of the way in which mechanical irritation, applied directly to a nervous trunk, acts, in the case when we chance to strike the ulnar nerve against any hard body; the pain that results is felt in the hand, and in every part to which the nerve sends branches. When muscular nerves are stimulated, contractions or spasms are induced, which continue so long as the stimulus is applied, and in some cases, for example, in the structures supplied by the sympathetic nerve, even after the stimulus is removed. The force used, or injury done to the nerve, being so great, that its substance is destroyed, sensation and motion, or the capacity to transmit these is annihilated. 2*d*, CHEMICAL STIMULI. All acrid, corroding substances, such as alkalis, many salts, acids, etc., act precisely in the same way as mechanical stimuli; they must never of course be applied of such strength, or in such quantity, as to destroy the organic substance, otherwise, their influence as stimulants is gone. 3*d*, THE STIMULUS OF TEMPERATURE. Within certain limits neither heat nor cold appears to have any peculiar action upon the sensitive and motory fibres; in excess, however, they affect the nerves power-

fully: ice, cold-water, and the contact of a red-hot wire, occasion as energetic contractions in the muscles, as they give rise to severe pain in the nerves of sensation. [The continued application of more moderate degrees of cold, is universally known to blunt sensation and to paralyse the muscles.] 4*th*, ELECTRICAL STIMULI occasion similar phenomena. The shock which is felt on taking a spark, or discharging a Leyden phial, is a consequence of the electrical stimulus, and is the expression of the pain which accompanies the sudden and violent contraction of the muscles. Electricity, particularly galvanic electricity, appears to affect the muscular nerves in an especial manner; these nerves are indeed extremely delicate electrometers, a fact that is proclaimed by the excitement of muscular contractions by the electrical tension that is induced by the simple contact of heterogeneous metals. The contractions are observed to follow at the moment of completing, and again at that of breaking the circle; with the latter, however, the contractions are of much less extent than with the former, and sometimes they are not induced by it at all. So long as the circle is kept complete, all contractions cease. Electricity in excessive force, as in lightning, in the shocks of very large electrical machines and galvanic batteries, do not act as stimuli, but kill or destroy the nervous substance and the nervous influence at once, like all overpowerful stimuli of other kinds[471]. 5*th*, The so styled INTERNAL ORGANIC, and farther, PATHOLOGICAL STIMULI, are for the most part referable to one or other of the categories already indicated; but they are still in some measure peculiar. The pain that accompanies inflammation, depends mainly on the mechanical pressure of the distended vessels upon the sensitive nervous fibrillæ. Spasms connected with the presence of worms in the intestines, with impressions of cold, and changes of external temperature, may be explained in the same way. The peculiar primary nervous actions that accompany certain pathological states, such, for example, as the feelings of heat and cold in febrile paroxysms, the pain in the pure neuralgiæ without mechanical or other injury, etc., must be referred to

[471] In connexion with the subject of the electrical stimulus, see A. v. Humboldt's work, *On the Excited Muscular and Nervous Fibre* (*Ueber die Gereizte Muskelund Nervenfuser*, 2 Th. Berol. 1797-99.), and Jo. Müller in *Encyclopæd. Worterbuch*, and his *Physiology*.

pathological stimuli of an organic kind[472]. A medium and due degree of stimulation appears to be maintained by the normal circulation of the blood, which indeed is altogether indispensable to the action of the nervous system. The loss of a large quantity of blood may be followed by almost every form of nervous derangement; for example, shivering, sparks before the eyes, head-ache, momentary or persistent blindness, syncope, convulsions, paralysis of the central portions of the nervous systems, insanity, etc. [473].

§ 241. The nerves may in a variety of ways lose their power of reacting, under the influence of stimuli, temporarily or for ever; they may be brought into a condition in which the nervous influence shall cease to operate, yet without any destruction of their substance, such as is occasioned by extreme mechanical violence and corrosive chemical agents. A blunting or diminution of the nervous irritability must therefore be acknowledged, and this may increase to its entire suspension or annihilation; the state which then exists is that of complete paralysis.

Paralysis of nerves may be induced: 1*st*, By over excitement, or excitement continued too long, consequently from internal or external incessant stimulation. By continuous moderate galvanization of a muscular nerve, its reaction becomes weaker and weaker by degrees, and by and by it ceases entirely; but with rest, the nerve [muscle] gradually recovers itself, and will again respond to the stimulus of the shock. In ordinary life such exhaustion of the nervous irritability or susceptibility is familiarly known to follow in the eye from the too incessant excitement of bright light, in the ear from the admission of over loud or long continued noises, in the brain from over-application and anxiety, in the spinal cord from over-indulgence of the sexual appetite, in the muscular system by over-exertion—men over-tasked, animals over-driven, lie down at last to die, having lost all power of farther effort. In many cases the irritability would seem rather to increase in the first instance, (exalted sensibility,) only to become blunted the

[472] See farther on this subject the General and Applied Physiology. The work of Romberg, *On the Nervous Diseases of Man*, (*Lehrbuch der Nervenkrankheiten des Menschen*, Berlin, 1840,) must be mentioned as a pathological *chef d'œuvre*, based on the latest researches into the physiology of the nerves.

[473] On the influence of the blood upon the nervous system, see the excellent treatise of Dr. Marshall Hall, *On Blood-letting*, in which the most interesting observations and experiments are brought together.

more quickly and completely afterwards. 2*d*, By long separation of the nerves from the brain and spinal cord, they lose their properties of reacting under stimuli,—of occasioning sensations, or causing contractions in the muscles. This fact is readily demonstrated by experiment: if a portion of a nerve be removed in a living animal, stimuli applied after a certain time to the remote end of the wounded nerve, excite no contractions in the muscles to which its branches are distributed[474]. 3*d*, There is a peculiar class of substances which possess the property of rendering the nervous influence very rapidly inoperative, without inducing any manifest change in the anatomical state or relations of the nervous substance—this at least must be owned in the present state of our knowledge.—These are NARCOTICS. They seem, as the general rule, to blunt after having powerfully exalted the sensibility, particularly of the central parts, for a brief interval previously. To this excitement complete paralysis succeeds[475]. The effect of narcotics is in many cases so rapid, however, that the period of excitement is almost inappreciable. Narcotics may operate in two ways; (*a*) By being taken up into the circulation, therefore indirectly; and (*b*) By being applied immediately to the tissues, and, therefore, directly. (*a*) When poisonous substances of peculiar intensity, such, for example, as hydrocyanic acid, strychnine, coniine, the poison of serpents, etc., are thrown immediately into the blood, or

[474] For farther development of the points here touched on, see the *General Physiology*. It is obvious that with all exalted reaction there is a greater expenditure of the nervous influence than in the normal state, and that this is followed by feebleness and exhaustion, until by repose and the renovation of the blood from the chyle, the nerves have had adequate supplies of the element necessary to their nutrition afforded them.

[475] Sticker and Müller have made experiments on this matter; vide the *Archiv* f. 1834, p. 202. Experiments on rabbits showed that when nerves which had been divided did not again coalesce, the peripheral or distal portions lost their susceptibility to mechanical and galvanic stimuli entirely, or in great measure, in the course of two months; the muscles to which these nerves were distributed also lost their irritability in the same period. In making this experiment it is found necessary to remove a piece of the nerve completely, in order to withdraw the peripheral portion of the nerve more certainly from the influence of the central masses; if this be not done, the upper and lower divided extremities of the nerve soon grow together, or become connected by means of an intermediate substance in which new nervous fibrils are produced, whereby the capacity of conduction is restored. (See § 239.) In the experiments referred to, the animals remained to the end paralyzed.

even taken into the stomach, in most cases paralysis of sensation and motion of the entire organism, and death, follow with singular rapidity. In such circumstances, the poisons dissolved in the blood almost always operate immediately upon the central portions of the nervous system, the entire mass of blood being simultaneously and very rapidly altered. The nerves and muscles nevertheless sometimes preserve, for a longer or shorter space of time, the faculty of reacting under the application of local stimulants. Frequently, however, this local susceptibility to stimuli is very speedily annihilated[476]. (*b*) When narcotic substances are brought into immediate contact with the living tissues, as when a solution of belladonna is dropped into the eye, or when the nerves or muscles of an animal are moistened with a solution of opium, or other powerful narcotic, the nerves lose their capacity of reaction very rapidly, and the muscles soon cease from contracting under the influence of mechanical, galvanic and other stimuli[477].

[476] This is always seen in the course of the experiments upon frogs with strychnine, described in § 215 : violent clonic and tonic spasms are first induced. The slightest movements, merely shaking the table or vessel on or in which the animals are placed, occasions renewed and aggravated spasms, so long as the power of reaction remains. The same thing occurs when birds and mammals are the subject of experiment; a dose of strychnine, coniine, or prussic acid, is followed, in the first instance, by spasms in the most dissimilar and distant parts, more or less remarkable, according to the nature of the poison; and it is only after these that paralysis and death ensue.

[477] The investigation of the *modus agendi* of narcotic poisons upon the central parts of the nervous system, after their reception into the circulation, is a subject of the highest interest. The symptoms or phenomena which manifest themselves in the different organs of motion, have been particularly noted, and I shall here briefly recapitulate the particulars of a series of experiments performed some time ago. A strong dog, several years old, had 25 drops of a solution of nitrate of strychnine (5 grs. to ℥ss of spirit) injected into his right pleura through a puncture in the side; as no phenomena were manifested after the lapse of five minutes, 40 drops more of the same solution were injected; a minute after this the extremities began to be twitched with spasms, immediately after which, the whole body became rigid, the four extremities being stretched out ; then for an interval of four minutes, there was an alternation of tonic and clonic spasms, particularly trismus, with alternate opening and shutting of the mouth, trembling of the tongue, rolling of the eyes; at first, there was discharge of urine, by and by, of feces, and finally, of mucus from the mouth. Four minutes later death took place with relaxation of every part. On opening the abdomen, the peristaltic motion of the intestines, normal in the first moment, was increased by the action of the air.—In an owl, 25 drops of the same solution thrown from behind into the lung, occasioned clonic spasms within one minute;

CHAPTER III.

Of the Functions of the Several Nerves.

§ 242. The first step towards a right understanding of the function performed by each nerve, was taken by Charles Bell. From simple observation of the anatomical distribution of the nerves, and the morbid phenomena he met with in the course of

the animal sunk in a state of collapse, opened its beak repeatedly, then became tetanic, and in three minutes died. A frog being the subject of experiment, a similar dose of the same poison was followed in half a minute by general tonic spasms, then by a tremulous motion in many muscles individually; half an hour later, and when the tetanus had ceased, convulsions were reproduced when the animal was touched. A puppy, 3 weeks old, had 20 drops of a watery solution of strychnine administered to it. Five minutes afterwards the bowels acted copiously, and the whole body shook or trembled without other ulterior phenomena. 25 drops of an alcoholic solution of strychnine (2 grs. to ʒi.) were then injected through a wound in the skin, after which, with the exception of a general rigor or shivering fit, no effect was produced; half a minute after 25 drops more of the same solution had been thrown into the cavity of the pleura, symptoms of trismus and tetanus supervened; a great quantity of saliva was discharged, and the pupils were much dilated; in ten minutes the irritability, which had been powerfully exalted at first, was extinguished, and the animal died. On opening the abdomen, peristaltic motions were set up vigorously in the intestines, and were still farther increased in energy when the cœliac plexus was touched with a solution of caustic potash; the motions of the heart continued for 30 minutes, as did the contractions of the diaphragm, when the phrenic nerve was irritated; the nerves of the extremities showed no reaction under the application of stimuli. A dog of the same age as the last had 30 drops of a solution of coniine (10 grs. to ʒvi alcoh.) thrown into the cavity of the thorax; in two minutes single clonic spasms supervened, then very violent opisthotonos, next trismus, and in five minutes, death; irritability of parts, as in last case. The following experiment shows how very differently the irritability stands affected in different cases after poisoning with narcotics, even in the same kind of animal: A number of frogs of the same size and vigour were killed with strychnine, (25 drops of a sol. of 2 grs. to ʒiss of the menstruum); the tetanus was observed to supervene with almost like celerity whether the poison was given by the mouth, insinuated under the skin, applied immediately to the spinal marrow, &c., and whether the animal was decapitated or not. In the greater number, the irritability in the nerves of the leg was found extinguished very shortly after death, and was not to be aroused by galvanism (at least not with the force of a single pair of plates); in several some slight reaction was still apparent, and in a few the irritability was conspicuous an hour after death. One frog, poisoned with coniine, died without tetanic spasms after a couple of

his practice, this distinguished individual was led to perceive that the nerves of every organ were numerous or complicated, in proportion to the number or complicated nature of its functions. He discovered that the anterior roots of the spinal nerves possessed merely motory powers, and that the posterior roots, provided with a ganglion, were endowed with the faculty of sensation alone. The resemblance of the fifth cerebral pair to the spinal nerves soon led Bell to the idea, that its roots, in all probability, possessed similar functions; and observations and experiments upon animals taught him that the sensibility of the face was due to branches derived from the larger root of the fifth, whilst its voluntary motions were all dependent on the *portio dura* of the seventh pair[478]. The path was now opened to a new physiology of the

convulsive throes; the sciatic nerves in this case remained long irritable. In all, the heart continued to beat for a great length of time. Frogs from which the heart had been removed, and to which strychnine was applied without producing any of its peculiar effects, (vide § 215,) retained their whole irritability long after death.

Müller dissected the femoral nerve of a frog free from all surrounding parts for a considerable distance, and then applied a solution of acetate of morphia to it; after a time the end of the nerve had completely lost its power of manifesting irritability. The same thing happened when muscles were placed in a solution of opium. Alexander von Humboldt observed the pulsations of the heart to become first extremely rapid under the influence of tincture of opium, and then to cease entirely; Müller's experiments show that the narcotizing effects of opium are limited to the parts to which the drug is applied; that they do not extend to the rest of the system. [The drug being received into the circulating system, of course exerts its specific effects generally, inasmuch as it is by this means applied generally. R. W.]

478 Bell's first inquiries date prior to the year 1811, when he printed and circulated privately a little tract entitled: *An idea of a new Anatomy of the Brain, submitted for the Observation of the Author's Friends.* At a subsequent period, his researches were laid before the Royal Society in a series of six papers, which may be found printed in the *Philosophical Transactions* between 1821 and 1829. These papers were afterwards collected by the author, and published with additions, under the compendious title: *The Nervous System of the Human Body, embracing the Papers delivered to the Royal Society*, 4to. Lond. 1830.

Magendie avers, that he had independently, and by the way of experiment, discovered in the year 1822 that the division of the posterior roots of the spinal nerves was followed by the cessation of feeling only, the division of the anterior roots by the loss of motion. *Journal de Physiologie Experimentale*, tom. ii. p. 276; and in Desmoulin's *Anatomie et Physiologie des Systèmes Nerveux*, Paris, 1825, tom. ii. p. 777; and there is no question but that Magendie, who experimented on warm-blooded animals, confirmed by vivisections the views entertained by Bell.

nervous system, which has found numerous labourers in very recent times; and, however contradictory and imperfect many observations still remain, however slow our actual advances in the knowledge of particular facts, may have been, we can already predicate

Jo. Müller has the merit of having shown the facility with which such experiments can be performed on frogs, and the striking results which, when rightly set about, they always afford—Froriep's *Notizen*, Marz, 1831, No. 646-647, reprinted with additions in Romberg's *Translation of Bell*, and the experiments extended to several of the cerebral nerves. [It is only fair to mention the names of Drs. Gall and Spurzheim, and of Mr. Alexander Walker, in connection with the History of Discovery in the Anatomy and Physiology of the nervous system. The two distinguished men first named, in their joint memoir addressed to the French Institute in March, 1808, insist particularly on the mutual independence, both anatomically and physiologically, of the several parts of the nervous system; the third corollary which they deduce from their anatomical discoveries, is to the following effect: "That there are as many particular systems, as there are different functions, but that all communicate by anastomoses." This doctrine is obviously the most general expression of that which is now universally received; and it is quite certain that the teaching and writings of the two German anatomists had immense influence upon the views of their cotemporaries, in regard to the structure and functions of the nervous system. Reil resumed his long neglected study of the Anatomy of the Brain after their visit to Halle in 1805 or 1806, and, in fact, adopted and exposed their views of the structure of the cerebellum and brain in the series of papers which he published in his *Archiv für Physiologie*, for 1807—08 and following years.

Mr. Alexander Walker, in two papers published in the *Archives of Science* in 1809, expresses himself in the following terms: "Now as in some cases sensation exists without volition," [he means the power to execute voluntary motions] "and as almost all nerves arise by distinct filaments, I am of opinion that, wherever a part having both sensation and motion is supplied from one nervous trunk, that trunk envelopes both a nerve of sensation and one of volition." * * "It is evident that two species of action take place through this [the medullary nervous] structure, one obviously advancing from the organs of sense towards the sensorium commune, and another returning from the sensorium commune to actuate the muscles and produce locomotion. Now it does not accord with the distinctness of natural operations to suppose, that these motions in opposite directions take place through one and the same series of particles; it is far more accordant with that distinctness to suppose that they take place through different series; and this becomes confirmed when we observe * * * the double columns of the spinal marrow, * * and the double origins, as they are termed, even of the encephalic nerves." The writer then goes on to state, that action commences in the organs of sense, and passes by the *anterior fasciculi* of the spinal nerves, which must therefore be nerves of sensation, whilst volition commencing in the cerebellum descends through the posterior columns of the spinal marrow, and expands through the *posterior fasciculi* of all the nerves, which must therefore be nerves of volition. Farther experience has not confirmed the *absolute* accuracy of these

with the greatest security a complete solution of all difficulties in the end [479]. Besides immediate anatomical investigation, carefully conducted experiments on animals just killed, rarely on living animals, are here of great importance. We here make use of a variety of subsidiary means, which are generally referable to the due application of stimuli, the effects of which have already been hinted at, (§ 240.) It is, indeed, in connexion with the functions of the nervous system, that experimental physiology has at this moment the widest theatre for display; neither does any part of physiology receive greater assistance from anatomical investigation, and the observation of morbid phenomena, than this.

views; but there is the broad principle of difference of office between the two roots of the spinal nerves asserted on anatomical grounds, and it was easy afterwards for any one to try whether the thing was so or not. Vide my addition to Annot. 525. R. W.]

[479] The first compendious and systematic view of the modern physiology of the nervous system, which is besides enriched with a multitude of new facts and important observations peculiar to the author, is contained in the third book of Müller's *Physiology.* After this, a number of important papers and publications made their appearance one after another, (for Müller's dissertatien had cleared the path for all to follow,) which contain various new facts in regard to the functions of the cerebral nerves, and which severally confirm, complete, or rectify each other. The following writers deserve to be particularly mentioned: Panizza, *Ricerche sperimentali sopra i Nervi*, Pavia, 1834, translated into German by Schneemann, Erlangen, 1836, (very important from the exhibition of the Glosso-pharyngeus as a nerve of taste.) Dr. Marshall Hall who has probably occupied himself more than any one else with experiments and speculations on the nervous system, has published a number of papers and works from time to time upon its anatomy and physiology. The last and most comprehensive is entitled: *On the Anatomy, Physiology, and Pathology of the Nervous System*, Lond. 8vo, 1842. Valentin, *De Functionibus Nervorum Cerebralium et Nervi Sympathici*, lib. iv., Bern, 1839, 4to. In this important work, not only are the observations of all previous inquirers passed in review, and made use of, but many new views peculiar to the author are exposed, and the results of his multifarious experiments given. The functions of the central masses are not discussed. Volkman has very recently instituted inquiries upon a very extensive scale, and in part made known the results he has obtained: *On the motory influences of the cerebral and cervical Nerves* (*Ueber die motorischen Wirkungen der Kopf-und Halsnerven,*) in Müller's *Archiv* f. 1841. Budge has also commenced a series of experiments: *Researches on the Nervous System*, 1st part, (*Untersuchungen über das Nervensystem,*) Frankf. 1841. Stilling of Cassel made known a few of the conclusions to which he had attained from his numerous experiments, at the assemblage of Naturalists that took place at Brunswick, in 1841, and has

Means and Appliances for Conducting Inquiries.

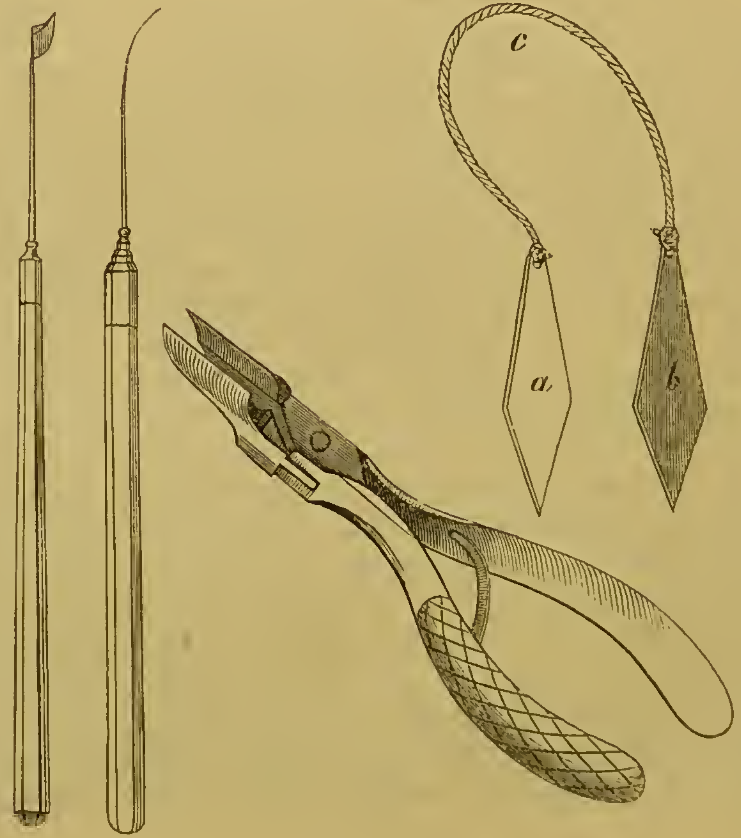
§ 243. Experience has shown that in conducting experiments, the right use of various means of excitement or stimulation, may be of the greatest importance; and that, on the contrary, many errors have arisen from the employment of inappropriate or insufficient agents and apparatus. It therefore seems proper in this place to point out the most necessary implements and methods of procedure, by the due use of which, the wished-for ends may be most surely attained, and every one be in a condition, without any great charge for tools, to repeat and test recorded experiments, and to make new ones for himself[480]. For the principal experiments,

communicated them to the author of this work in MS. Van Deen, whose varied and highly important inquiries are collected in his work, entitled, *Traités et Découvertes sur la Physiologie de la Moëlle épiniere*, Leide, 1841.

[480] As the instruments necessary in conducting experiments upon the physiology of the nervous system are not generally known, I shall here supply a short account of them. In laying open the spinal canal of frogs, a pair of cutting pliers of the fashion of those figured below will be found extremely useful. With such an instrument, the muscles having been previously removed, it is easy to cut away the vertebral arches behind, or the bodies of the vertebræ before, and so to expose the spinal cord either on its dorsal or abdominal aspect. Pliers of the same kind, of a larger size, will be found the best instruments for laying bare the spinal cord of rabbits, dogs, &c. For the mechanical stimulation of the nervous roots, and of any point upon a cut surface of the brain or spinal cord, it is well to be provided with a needle mounted on a light handle (Fig. 2). This needle should be of soft, not of tempered steel, so that it can readily be bent in different curves, and so made to serve for raising the roots, or particular filaments of nerves which we would stimulate, or snip through with the scissars. This implies, that scissars of different sizes and fashion, mostly of delicate construction, both straight and curved, with fine points and knife edges, similar to those that are made for the performance of operations on the eye, should be at hand. Stilling recommends small but strong scissars, with short blades bent at an angle, as convenient for getting at the spinal cord of frogs, &c. To open the cranium of rabbits quickly, and at the same time to remove a portion of the included brain, Stilling uses a strong sickle-shaped blade, in the fashion of a pruning knife. A very useful, in many cases even an indispensable instrument, is the Neurotome. (Fig. 3.) It is a small knife of such strength and fashion that it can be forced through the bony covering of the brain, in the smaller animals, and made to reach with the least possible amount of injury, the nerves at their roots or origins. Among chemical stimuli, caustic

frogs afford the best subjects; for those having reference to the cerebral nerves, rabbits and dogs among the mammalia are generally

potash, and strong acetic acid, will probably be found the best and most convenient in the greater number of instances. Acetic acid in particular, is an excellent irritant; it is easily applied of any strength, by means of a finely pointed glass rod, to whatever part seems desirable. Some kind of galvanic apparatus is altogether indispensable; probably the most useful of any, will be found a simple pair of plates, and the form delineated in Fig. 4, is greatly to be commended. It consists of a plate of copper well beaten and polished, of a pointed lozenge shape, *a*, and of a plate of zinc, of the same shape, *b*, connected by means of a silver, or plated copper wire, in such a way, that the two poles can be brought close together, and applied to a particular point, or being separated can be made to include a certain extent of parts in the circuit. This very feeble apparatus is still capable, on the circuit being closed, of exciting the strongest contractions in the muscles of the whole hinder extremity of a frog, through the entire extent of the diaphragm in a rabbit, &c. In employing galvanism, it is always proper to begin with a single pair of plates; with an apparatus of no greater power, the specific function of the two orders of roots arising from the spinal cord can be demonstrated; whilst with a more powerful system, all becomes confusion, the galvanic fluid being in such quantity as to pass from one root to another. It is often necessary, however, to have a greater current than is produced by the single pair of small plates, for instance, in



chosen[481]. It will not be held impertinent if I here observe, that in many, in the majority of cases, experiments performed upon animals but just killed, yield less complicated and more decisive results, than such as are instituted on living animals[482].

trying the state of the excitability in the muscular nerves of animals that have been dead for some time, or of parts that have been, for a longer or shorter period of time, entirely separated from the body. In many subjective experiments, for example, on the irritability of nerves of sense, an inductive apparatus, such as may be found described in the ordinary text books of natural philosophy, is the most convenient; I have myself found the inductive multiplier of Ganss and Weber (Gehler's *Dictionary of Physics*, vol. ix., p. 120, Fig. XV.) extremely available; experiments of the most varied kind can be undertaken by its means, and as it is capable of nice regulation, yet works with very considerable energy; as it is easily kept in order, and requires little or no trouble in cleaning, getting ready, &c., it is much to be recommended.

[481] Frogs are particularly available for many of the experiments, which will be indicated by and by. They must, however, be lively and vigorous. In very hot weather they are not such good subjects as when the temperature is moderate. It is seldom necessary to go higher than the harmless rabbit; although in some cases dogs are more available. The larger mammals are seldom required; [when they are, the donkey, and the horse at the knacker's, are the subjects generally selected.]

[482] In the interest of true science, and on the score of humanity, it should be the business of every physiologist carefully to avoid the infliction of unnecessary pain. The cruellest experiments have hitherto been the least fertile in results, and for this obvious reason, that in inflicting severe wounds, particularly when they were accompanied with a considerable loss of blood, which happens so constantly, animals are brought into a condition in which it is generally impossible to say how far any manifestation of pain or irritability is referable to the general procedure, or to any particular act in its course, such as the division of the root or branch of a sensitive or motory nerve, &c. It is quite indisputable that very few satisfactory results have accrued from the barbarous experiments of the Parisian School of Physiology, whilst Bell actually arrived at all the main facts in his discoveries without any vivisection whatsoever! In researches into the motory powers of nerves, we without exception proceed to much greater advantage, and with much greater certainty, upon the bodies of animals just dead—put to death by hanging, poisoning, or decapitation. As it is known that those nerves which subserve motion when touched with a simple pair of galvanic plates, cause contractions or other motions in the muscles or parts which they supply, we may often legitimately infer that nerves which do not produce any such effects, when they are galvanized, are nerves of sensation. It may seem unnecessary to insist on the greatest care and foresight in making every experiment; but the singular discrepancy which is notorious among experimental physiologists, and the diversity of results obtained and conclusions formed from precisely similar series of experiments in different hands, ought to satisfy us of the great liability under which we lie of being deceived. In all cases experiment ought to rest on the broadest anatomical basis, and the results to be contrasted with those of pathological inquiries. Some excellent remarks on *Observation* and *Experiment* will be found in Dr. Marsh. Hall's *Critical and Experimental Essay on the Circulation*, 8vo. Lond. 1831.

Of the Nature of the Higher Nerves of Sense.

§ 244. All nerves of sensation when impressed or stimulated, do not give rise to like sensations. The three higher nerves of sense—the olfactory, optic, and acoustic nerves, have no sensations of pleasure and pain; they do not distinguish the relative temperatures which we call hot and cold, etc.; they only experience, or give rise to, sensations of odour, light, and sound. Stimulation, or irritation of the most varied description, mechanical, chemical, electrical, internal organic,—that which results from congestion, for example,—etc., excites only sensations of light and colours in the optic nerve, of sounds or noises in the acoustic, and of smells in the olfactory; and it is the same in regard to every one of the special nerves.

§ 245. That the olfactory nerve is the seat of smell; and farther, that it has no other function but this, is altogether unquestionable. Experiments satisfy us, that it has no fibres of common sensation: is the nerve divided, the sense of smell ceases completely; but common sensation remains in the parts to which it is distributed[483]. The sense of smell is sometimes wholly wanting in men, otherwise perfectly healthy; and in these cases, some degeneration or primary failure of the nerve has been discovered[484].

§ 246. Anatomical and pathological observation, as well as direct experiment, demonstrate beyond all question, that the optic nerve is exclusively the instrument by which sensations of vision are excited. Animals in which the optic nerves are divided, immediately become blind, and remain so, although the divided extremities of the nerves may coalesce and heal[485],—no trace of the faculty of visual perception remains. The optic nerve irritated in any way, the sensation excited is that of light[486]. On the other hand, the

[483] Magendie and Valentin have both performed experiments upon animals which irrefragably prove this fact. The animals (rabbits) remained quite tranquil after Valentin's experiments, in which the olfactory nerves were divided with the neurotome;—they all survived the injury done them.

[484] The pathological cases that bear upon this point have been collected by Valentin, l. c. p. 11. See farther under § 284 et seq. where the sense of smell is particularly discussed.

[485] Here, therefore, is an exception to the rule (§ 239) according to which the function in divided nerves is restored on their continuity being re-established. It would seem as if the same rule held good, in reference to all the nerves of special sense.

[486] On this point see the Chapter on Vision.

sensibility remains unimpaired in all the parts of the eye-ball, and in its coverings, after the section of the optic nerves. Motion never follows the irritation of the optic nerves; occasionally, however, a contraction of the pupil occurs at the moment that section of the optic nerves is performed[487], in consequence, as it appears, of a reflection influencing the oculo-motorius. The contraction of the pupil in question also ceases very shortly after the division, and it is then as insensible to the stimulus of light, as the retina itself.

§ 247. Direct experiments cannot be made on the auditory nerve of living animals, by reason of the depth at which it is placed, and the nature of its coverings. But injury, destruction by abscesses and atrophy of the nerve, occasion deafness; and internal stimuli and mechanical irritation always excite subjective acoustic sensations[488].

Functions of the Muscular Nerves of the Eye.

§ 248. The opinions of physiologists do not seem yet completely made up in regard to the nature of the muscular nerves of the eye. The THIRD PAIR,—nervus oculomotorius,—is certainly the principal nerve of motion of the muscles of the eye; but it would seem to include sensitive as well as motory fibres. The two functions are perhaps attributes of its external and internal principal constituent portions[489]. The motory fibrils are distributed to five, or even six of the muscles of the eye. The rectus superior, r. internus, r. inferior, the obliquus inferior, and perhaps also the obliquus superior[490]. The third nerve is also the motory nerve of the

[487] Valentin remarked it in the dog and rabbit.

[488] Vide on the last point in particular the Chapter on Hearing.

[489] Vide Valentin's *Neurology* in his ed. of Söemmerring's *Anatomy*, p. 325, and *De Functionibus Nervorum*, &c., p. 17. The conclusion that the nerve contains sensitive fibrils in considerable number, is based on the observation, that rabbits in whom the third pair is divided, even in the interior of the cranium, give indications of acute suffering.

[490] Contractions of all these muscles take place upon irritation of the nerve, and paralysis upon its division; ptosis, or falling of the upper eyelid, is also a consequence of its section. According to Volkmann, (Müller's *Archiv*, 1840, S. 477,) when the root of the nerve is irritated in the calf, sheep, and cat, contractions also take place in the obliquus superior, and retractor-bulbi muscles; and both muscles, as it seems, receive twigs from the third pair; contractions have also been noted in the rectus externus, by the same observer, a fact which

iris[491]. Indirect or reflex motions of the parts to which the oculomotory is distributed, are occasioned by irritations of the optic nerve; such motions cease the moment the trunk of the oculomotory nerve is divided[492].

§ 249. The FOURTH PAIR—N. trochlearis seu patheticus appears to consist of motory fibrils only; the presence of sensitive fibrils at all events is still doubtful, and in any case they must occur in very small numbers[493]. The nerve regulates the motions of the superior oblique muscle; contractions in any of the other muscles of the eye, never follow irritation of its roots[494].

§ 250. The motory function of the SIXTH PAIR—N. abducens—is unquestionable; this has been abundantly proved, both by pathological occurrences and direct experiments. Its action is restricted to the external straight muscle of the eye[495]. Whether it contains any sensitive fibrils or not, cannot be positively ascertained; inasmuch as the passage of the neurotome necessarily implicates other parts[496].

Functions of the Fifth Pair.

§ 251. The widely distributed FIFTH PAIR—N. trigeminus—upon the functions of which we possess very comprehensive obser-

is perhaps to be explained from the accessory or strengthening twig which the nerve gives off in the calf to the fourth pair.

491 At the instant of dividing the trunk of the nerve, according to Valentin, the pupil of the corresponding eye is powerfully contracted; that of the opposite eye is very commonly similarly affected also; by and by the pupil dilates and remains paralysed.

492 The motions of the iris in man and mammalia are all involuntary. In birds, again, the pupil is contracted and dilated at the will of the animal. The iris also receives motory fibrils from the sympathetic, which act as antagonists to those of the oculomotory. Valentin thinks that the superior branch of the oculomotory nerve excites for the major part only voluntary and reflex motions, whilst the inferior branch is connected only with involuntary and reflex actions.

493 Valentin (Söemmerring, S. 239) opines that this nerve contains very few sensitive fibrils. How difficult it is to conclude definitively on this point, however, may be seen by referring to his *De Funct. Nerv.*, p. 21. It is very difficult to make satisfactory experiments upon the fourth pair, by reason of its tenuity, and the depth at which it is situated. Animals cry out when it is divided, but this may be owing to unavoidable pressure upon or interference with the N. trigeminus.

494 See Volkmann, l. c., p. 480.

495 Paralysis, or division of the nerve, is followed by squinting inwards, in consequence of the preponderance which now attaches to the rectus internus.

496 Vide Valentin, *De Funct. Nerv.*, p. 30.

vations, is a mixed nerve, a fact which the anatomical characters at its origin would lead us to expect. It arises by a great external root, (portio major,) which still included in the cavity of the cranium, expands into the Gasserian or semilunar ganglion, and by a smaller root, (portio minor,) which lies to the inside of the former. The resemblance which this structure bears to that of the spinal nerves, is obvious; but there is this anatomical difference between them, that in the fifth, the fibres from the two origins do not intermingle after their conjunction. In the third branch of the fifth, indeed, there is a greater resemblance to a spinal nerve, for here, the fibres from the two sources do interlace to a certain extent at least.

Little doubt now prevails in regard to the functions of this nerve, so accessible both to observation and to experiment; the slight differences that exist among physiologists refer to a few particular branches only. In conformity with the anatomical arrangement, direct experiments and pathological cases satisfy us that the greater posterior or ganglionic portion of the nerve is made up of sensitive fibrils, whilst the smaller internal or ganglionless portion is made up of motory fibrils. The former of these roots obviously corresponds with the posterior root of the spinal nerves, the latter with the anterior root of the same nerves. The root of the smaller anterior or ganglionless portion of the fifth nerve, when galvanized in an animal but just dead, excites powerful masticatory movements in the jaws, so that the teeth are snapped and ground together. When this root is divided in a living animal, the lower jaw falls,—paralysis of its muscles is induced; when the section is made on one side only, the jaw loses its parellelism, even in a state of repose, but particularly during the action of chewing. The branches of the smaller anterior portion of the fifth pair appear to be distributed exclusively to the muscles of mastication; the most recent and careful observation seems to prove that it has no part in the motions of the cheek, lips, or soft palate[497]. Excitation, or stimulation, whether of the greater root of the fifth, or of any other cerebral nerve, has not been seen to excite motions of mastication.

When the greater or ganglionic portion of the fifth nerve is

[497] This from the decisive and numerous experiments of Volkmann, Müller's *Arch.*, 1840. S. 485. [Mr. Mayo appears to have been the first who demonstrated the precise function of the 2d branch of the 5th pair; in doing so, however, he must be held rather to have corrected an error into which his preceptor, Bell, had

divided, animals howl and give extraordinary indications of suffering pain; and after the operation, the integuments of the forehead, temples, eye-lids, nose, mouth, and greater part of the ear, the conjunctiva, the mucous membrane of the nasal fossæ, of a great part of the mouth, and of a portion of the upper surface of the pharynx, the surface of the tongue, the teeth, and the gums, are all deprived of sensation, whilst the faculty of muscular motion remains unimpaired.

With reference to the particular branches of the nerve, the first or ophthalmic branch, appears to comprise sensitive fibrils only, so that its paralysis, or division, is followed by the cessation of feeling in the parts to which it is distributed—the nervi æthmoidales are thus found to confer sensibility on the mucous membrane of the nose. The second or maxillary branch of the fifth, also includes sensitive fibrils only[498]. The sensibility of the infra-orbitary subdivision of this branch, is most easily demonstrated by the way of experiment[499]. The third, or inferior maxillary branch, the common trunk of the lingual and dental subdivisions, is of mixed nature, but with a decided predominance of sensitive fibrils[500]. The superficial temporal branch is not merely sensitive, as was once believed, but contains a number of motory fibrils derived from the lesser portion[501]. On dividing the lingual branch, the sense of taste seems to remain completely unaffected. The dental branch is of mixed nature; but distributes the whole of its motory fibrils to the mylo-hyoideus muscle[502].

been led by his theoretical views, than to have taken an original path and made a discovery. See his *Anat. and Physiol. Comment.*, No. I. Aug., 1822. R. W.]

[498] This nerve gives off a branch of communication to the nervus abducens, which has a different origin, mostly from the plexus situated at the back part of the inferior orbital fissure (Augenhöhlenspalt); more rarely from the spheno-palatine ganglion (Gaumenkeilbeinknoten), and probably mingles some sensitive fibrils with the proper motory ones of the nervus abducens. (See Valentin in Söemmer., S. 564, and *De Funct. Nerv.*, p. 25.

[499] It is extremely easy to make this section in animals. This branch is very commonly the seat of the distressing and very violent pain which is usually spoken of under the name of *tic douloureux;* and transient or more permanent paralytic affections of the parts it supplies, in consequence of rheumatic or other attacks, are frequently met with by the practical physician; here the sensibility is more or less blunted, or destroyed, whilst the faculty of muscular motion remains in all its integrity.

[500] Vide Valentin, *De Funct. Nerv.*, p. 28.

[501] Vide Valentin, l. c.

[502] See farther on this point, the observations on the Glosso-pharyngeal nerve, and on the Sense of Taste.

§ 252. The great size and extent of distribution of the fifth pair, and its function as principal nerve of feeling to the organs of sense, give it a peculiar physiological importance. It is in fact the nerve of sensation to the nose, eye, ear, and tongue; and in the lips[503] and tongue it becomes the instrument of the special sensibility, which is characterized as touch. It is in close connexion with many of the mental emotions; it is the link in the act of kissing as evidence of affection or more material love, in the blanching or flushing of the cheek under such mental emotions as fear, rage, etc. etc. A great number of reflex motions are also dependent on its actions; whence the peculiar phenomena and mischiefs that ensue upon the atrophy or destruction of the whole nerve, or upon the division or injury of one or more of its particular branches. We have now so ample a collection of experiments and medical observations upon these points, that the various groups of pathological appearances encountered are susceptible of satisfactory analysis as well as reference to their true physiological causes[504].

[503] See farther on this point the Section on the Organ of Touch.

[504] The most important facts and experiments, as well as clinical observations illustrative of these matters, will be found in Magendie (*Journ de Physiol. exper. et Physiologie*). Vide Eschricht, *De Funct. Nerv. faciei et Olfactus*, Havn. 1826, [and particularly a paper by Mr. John Shaw, nephew and pupil of Charles Bell, "On partial paralysis," in *Trans. Med. Chirurg. Society*, 1822; also Bell's *Essay on a New Anatomy of the Brain*, 1811, and his subsequent writings. R. W.] Valentin has given a masterly exposition of the principal phenomena in his contribution to Sömmerring's *Anatomy*, of which the following is a brief abstract: After the destruction of the sensibility by the division of the greater or ganglionic portion of the nerve, no reflex motion occurs; the mucous membrane of the nostrils being stimulated by mechanical means, there is no sneezing; no increased flow of tears, and no closing of the eyelids when the conjunctiva is irritated; no augmented secretion of saliva on stimulating substances being taken into the mouth, &c. Immediately after the division, rapid movements—mostly contractions—take place in the pupil, which in the dog and cat becomes extremely small, and remains so under every variety of circumstance. With reference to the changes that ensue in the nutritive processes, inflammation of the eye was the first phenomenon that appeared, being accompanied by increased secretion of mucus, and then by the elaboration of purulent matter. Ulcerations of the cornea next occurred, and then collections of matter in the anterior chamber; the cornea often gave way, and the whole contents of the eyeball then escaped. Dry crusts, meanwhile, were formed upon the lips, and sometimes on the chin and nose; in dogs the tongue often became covered with a thick fur. The same things have been observed in man; but the play of the features in expressing affections and passions remains uninterrupted; of course anything that is brought into contact with the paralysed side or part is not felt; the patient when he drinks has the impression as if a piece were broken out of the glass or cup, &c.

Facial Nerve (portio dura of the Seventh Pair.)

§ 253. It is through the facial nerve, (portio dura of the seventh pair,) that the play of the muscles of the face is effected; it enables the countenance to assume the varied expression characteristic of the different affections and passions. When this nerve is galvanized, the whole of the muscles of the face and ear are thrown into the most active contractions; whether the muscles of the palate be similarly influenced or not, has not been exactly ascertained[505]. When this nerve is divided, as it used to be formerly in cases of tic-douloureux, when the physiology of the nervous system was less advanced than it is at present, paralysis of all the parts to which it is distributed, was the consequence,—all character and expression left the countenance;[506] and the salivary glands poured out their secretion less copiously than before. At its root the portio dura is a pure motory nerve; but after it emerges from the foramen stylo-mastoideum, it receives a few sensitive fibrils from the fifth and tenth pairs.

Glosso-pharyngeal Nerve.

§ 254. The views of different observers are singularly divided in regard to the function of the glosso-pharyngeal portion of the

[505] Valentin saw motions on one occasion in the soft palate; but he seems more lately to doubt whether this was not accidental (Soemmer. S. 462); Volkmann (l. c.) distinctly denies any such motions; on irritating the root of the nerve in the calf, dog, and sheep, he observed spasms in the musc. frontalis, buccinator, orbicularis palpebrarum, and orbicularis oris, and farther motions of the nose, of the angle of the mouth, and of the ear,—the attrahentes, retrahentes, and attolentes, being the muscles of the last named organ which were influenced —of the posterior belly of the digastricus, of the stylo-hyoideus and platysma myoides; he could not perceive any motions in the proper muscles of the ear.

[506] The consequences of paralysis of this nerve in the human subject are very remarkable; and the idea of destroying it as it escapes from the styloid hole in cases of tic-douloureux was a most unhappy one, (the operation was first performed by Klein of Stuttgardt; Siebold's *Chiron*, Bd. II. S. I): the patient is immediately made incapable of moving the skin of his forehead; he can no longer close his eyelids completely; he cannot breathe comfortably in consequence of the collapse of his nostrils; he cannot spit or sneeze; the saliva distils from the imperfectly closed corners of the mouth; the lower lip drops away from the jaw; and in all the various acts of speaking, eating, drinking, &c. many difficulties and impediments are of course encountered. The sensibility of all the parts remains, but the face is totally devoid of expression, whatever the mood of the mind.

eighth pair of nerves. All our additional information, however, leads us rather to regard it as the principal or as the exclusive nerve of taste, the hypoglossal or lingual being connected with the motions of the tongue only, whilst the lingual branch of the fifth confers common sensibility and also touch, which the tongue possesses in considerable perfection,[507]. The glosso-pharyngeal, which in its course receives fibrils from the third branch of the fifth, from the facial and from the par vagum, appears, in fact, to be a mixed nerve; its anatomy assures of this; for in man, mammalia, and birds, it very obviously arises by a double root, the thicker of the two being farther furnished with a ganglion[508]. No kind of motion is excited by stimulating this root of the nerve; which can be readily traced distributing its fibrils to the papillæ on the root of the tongue,—those papillæ that are endowed with the most exquisite sense of taste; on stimulating the thinner root of the nerve,—which by the way is very readily overlooked—on the contrary, powerful contractions are excited in the musc. constrictor faucium medius and stylopharyn-

[507] The views entertained some short time ago by Magendie, Bell, Mayo, Müller, Gurlt, and others—would have led us to regard the lingual branch of the fifth as the proper nerve of taste; but the conclusions of Panizza, Valentin, Hall, Broughton, Stannius, and myself, are in favour of the glosso-pharyngeal as the medium of this sense. Romberg styles it the nerve of instinctive taste. Vide farther on this point the two Sections on Taste.

[508] See the inquiries of Volkmann, (Muller's *Archiv* f. 1840, S. 488) to whom we are unquestionably most deeply indebted for information upon the anatomy and motory function of this nerve. He discovered the glosso-pharyngeal to arise by two roots in man, the dog, cat, and calf, each of which was readily resolvable with care into two fasciculi of radicles; the ganglion—which Volkmann, however, finds not to be very constant, and when present to be but a detached portion of the ganglion petrosum—belongs to the thicker root. Occasionally single or detached ganglionic cells are recognizable between the particular fibrils composing the roots, before they penetrate the substance of the ganglion. Volkmann's researches compel us at all events to admit, that the combined radicles of the glosso-pharyngeus pass through the substance of the ganglion, and it would therefore be unfair to liken the two roots of this nerve to the double roots of the spinal nerves, or to compare its ganglion,—the ganglion Ehrenritteri—with the ganglions of their sensitive roots. This view is calculated to arouse reflection; for all our researches into the mode of origin of the cerebral nerves have, hitherto, tended to show us more and more striking analogies to the spinal nerves, in the particulars of course and mode of distribution.

geus[509]. There can be no doubt therefore of the glosso-pharyngeal comprising motory as well as sensitive fibrils[510].

The Par Vagum, (N. vagus, N. pneumogastricus).

§ 255. Next to the fifth, among the cerebral nerves, the PAR VAGUM is that which has the most extensive distribution. Its extensive ramifications to the most dissimilar organs, and its numerous anastomoses with other nerves, make it very difficult to analyse the functions of this nerve, and indeed there are still many points about it which remain unsettled or disputed. When the law of the distinct origin of the motory and sensitive fibrils came to be generally received, many showed themselves disposed to regard the vagus and accessory of Willis, taken together, as the analogues of a single spinal pair, the vagus with its ganglion of course representing the posterior or sensitive root, and the spinal accessory, the anterior or motory portion[511]. In this way a mixed nerve, very similar to the trigeminus, was certainly composed, and the idea received pretty general assent from physiologists. The vagus now came to be almost universally regarded as a purely sensitive nerve at its origin, and was held only to receive motory fibrils from the accessory nerve in its course. The grounds upon which this was admitted are these: 1*st*, In the foramen lacerum the nerve enlarges into a ganglion, which bears a strong resemblance to that which occurs on the posterior root of a spinal nerve; 2*d*, No kind

[509] Volkmann found, in his experiments on the calf and cat, that stimulation of the glosso-pharyngeal excited contractions in these two muscles only, that no other nerve had any influence upon them, and that the thinner root was alone possessed of motory power.

[510] Dr. John Reid has given a very good summary of extant inquiries upon the structure and function of the glosso-pharyngeal nerve. On stimulating it he observed that he excited contractions in the pharynx, and in the muscles of the lower part of the face; he also inferred that the nerve was endowed with common sensibility, inasmuch as animals at the same time gave indications of suffering pain. (*Cyclop. of Anat. and Physiol.*, vol. ii., p. 494.)

[511] This beautiful theory, first propounded as it appears, by Goerres, (*Exposition of Physiology*, Coblenz, 1805,) was maintained on anatomical grounds by Arnold, (Tiedemann and Treviranus' *Zeitschrift*, iii. 148,) and Scarpa, (*Annali Universali*, 1831,) and farther illustrated by Bischoff by zootomical researches, the results of which are consigned in his admirable little work: *Comment. de Nervi Accessorii Willisii Anatome*, Darmst. 1832. Müller, Gaedechens, Bendtz, and Valentin, add the authority of their names to the same views.

of contraction or spasm of the pharynx or stomach ensues when the trunk of the nerve in the neck is stimulated, galvanized, etc.; 3*d*, It receives numerous filaments from the accessory, which is acknowledged to be principally or exclusively a motory nerve[512]. We shall see that the most recent inquiries proclaim the vagus as a mixed nerve, and that this view is supported by every anatomical and physiological consideration.

§ 256. It is perfectly certain that the par vagum in mammalia at least, has double roots, the greater number of which enter the ganglion, whilst a smaller portion passes over it[513]. It is still difficult to determine, however, whether all the roots of the vagus are not soon after their exit penetrated or enveloped by ganglionic masses[514]. In man, the vagus arises by numerous fasciculi from the middle tracts of the medulla oblongata; and these unite into a common trunk which enters the jugular fossa of the skull. So soon as the nerve has passed through the opening of the dura mater which transmits it, ganglionic globules are observed disseminated among its fibrils; these belong to the jugular ganglion, which appertains in major part or entirely to the vagus, though it is difficult to say whether or not, and to what extent, the spinal-accessory participates in its formation[515]; the posterior trunk of the accessory, at all events, appears to be excluded from the ganglion, whilst a few filaments of the glosso-pharyngeal, of the sympathetic,

[512] Vide Müller's *Physiology*, where the grounds are laid down; the author has, however, so far modified his views in his third edition, that he maintains the vagus, in major part, to represent the posterior root of a spinal nerve; but that it is by no means certain that this is so in every case, inasmuch as one experiment seemed to proclaim the presence of motory fibrils in this root, and because in some animals, pretty large bundles of fibrils pass from the root over the ganglion without mixing with it. Valentin holds the vagus originally for a merely sensitive nerve. (*De Funct. Nervor.*, p. 45; and Söemmer., p. 508.)

[513] Remak made this observation, so important in a physiological point of view, in dogs, cats, and rabbits, Froriep's *Neue Notizen*, 1837, No. 54. Volkmann also observed that a portion of the root of the par vagum passed over the ganglion in the dog and sheep; the union between the two parts being merely by cellular tissue, l. c., p. 491.

[514] Volkmann found ganglionic masses betwixt all the numerous roots of the vagus in the calf.

[515] Vide on this point Valentin in Söemmerring, p. 482. He says that occasionally there is the appearance at least of ganglionic masses penetrating into the anastomoses of the accessory. He thinks that the arrangement here may be different in different individuals.

and perchance of the facial also, appertain to it[516]. The accessory unites with the vagus during the passage through the jugular foramen, beneath the opening of the dura mater; the two nerves now combine, and become inextricably interlaced and connected.

It had still been doubtful whether the proper roots of the vagus were purely sensitive, or contained a few motory fibrils mixed with them. Very recent inquiries seem to confirm the accuracy of the latter idea[517]. When the nerve is divided, severe pain is always manifested[518]; but on stimulating the nerve after the division, movements have been observed to supervene in the very numerous and very various parts to which the vagus is distributed. These parts are the soft palate with its aggregate muscles; the superior and inferior constrictors of the pharynx; the œsophagus through its entire length; the stomach, and several of the muscles of the larynx[519]. By its speedy junction with the spinal accessory, a nerve exclusively or almost exclusively dedicated to motion, the vagus becomes a thoroughly mixed nerve, and in its entire subsequent course leaves us in no doubt as to the two-fold properties of its fibrils; the nerve moreover anastomoses with the cervical nerves, and with the sympathetic.

[516] So says Valentin, Söemmerring, p. 483.

[517] This is the inference from Volkmann's experiments, which were instituted with great care; also from Stilling's inquiries, communicated to me verbally and by letter, and from my own researches, which were repetitions of Volkmann's and Stilling's.

[518] Valentin states, *De Funct. Nerv.* p. 45, that even the slightest mechanical or chemical irritation of the divided root of the nerve in the living rabbit causes such violent pain, that the animal cries out wofully; these indications of suffering, however, do not last so long as after divisions of the root of the fifth pair. If the nerve be irritated whilst still connected with the brain, the ordinary reflex motions are produced.

[519] It is remarkable, as Valentin informs us expressly, that in the horse, dog, and rabbit, no motions were to be perceived either in the pharynx, œsophagus, or stomach, nor in the larynx, or trachea. Volkmann divided the roots of the glosso-pharyngeus and accessory nerve completely, and observed motions in the parts just mentioned, at the moment of dividing and irritating the several roots in the calf, sheep, dog, goat, and cat. He noted wrinkles in the muscles of the larynx, in the crico-arytenoideus posticus and lateralis in the cat, in the crico-arytenoideus posticus in the dog. Volkmann, on the other hand, is inclined to regard the motions which were observed in the stomach as secondary only, in as much as this part is obviously influenced by the powerful contractions of the œsophagus in the vicinity of the cardia. Stilling observed distinct motions in the œsophagus and stomach, and rima glottidis, on irritating the roots of the vagus:

§ 257. The branches of the par vagum mingled with the nerves already mentioned, extend to the posterior parts of the head, to the external ear and auditory passage, to the œsophagus, larynx, trachea, thyroid body, to the heart and stomach, and still farther, to the plexuses that surround the roots of the great arteries that supply the viscera,—the cœliac and superior mesenteric in particular—plexuses from which the whole of the abdominal viscera receive nerves. Through the whole of this extensive course, the vagus appears to confer sensibility: it is the nerve of sensation to the vocal and respiratory organs, and to the stomach. The sensibility here may be spoken of as two-fold in its nature: it is *common*—it excites in the mind pleasurable and painful sensations; and it is *specific*, and this is of two kinds,—the peculiar sensations of hunger and thirst in reference to the stomach, and of the necessity of breathing in reference to the lungs, are connected with it[520].

§ 258. With reference to the functions of the individual branches of the vagus, it may be said that the auricular branch imparts sensibility to the external parts of the organ of hearing. The œsophageal branches are mixed, i. e. they confer both sensation and motion; so are the two laryngeal branches; the superior, however, is for the major part sensitive, the inferior on the contrary is for the most part motory. When the superior laryngeal nerve is irritated, pain, and a slight tremulous motion of the mucous membrane of the larynx and chordæ vocales, which, however, has no effect upon the voice, are produced. The division of the recurrent nerve is attended with little or no pain; but it is followed by hoarseness, or aphonia, in as much as the greater number of the laryngeal muscles are immediately paralysed[521]. The other branches

and I have myself, under the same circumstances, seen progressive powerful motions of the stomach, proceeding from the cardia towards the fundus, follow the strong contractions of the œsophagus; these motions I could not regard as secondary, or as due to the stimulus of the air upon the parts just exposed to it.

[520] It is not my purpose here to speak of the categories of sensibility, or to inquire in how far the several primary nervous fibres, or the parts connected with each of them in the brain, stand related to the greatly diversified specific sensations of pleasure and pain, which, farther, according to the particular organs—such as the heart, stomach, genital organs, &c., exhibit the greatest variety of shades. These points I reserve for the General Physiology.

[521] On these experiments consult Valentin, *Op. Cit.*, and Volkmann. The latter saw strong contractions in the cryco-thyroideus and constrictor faucium superius in the cat; and in these muscles, and the hyo-thyreoideus in the dog

distributed to the thoracic viscera, are the sensitive nerves of the parts[522]. Division of the vagus or pneumogastric in the neck on one side, is not absolutely fatal; animals have survived the operation for years; when the nerve is divided in the neck or upper part of the chest, on both sides, the respiration is implicated, the necessary change in the blood is arrested, and death, therefore, necessarily soon ensues. Division of the nerves beneath the lungs, immediately above or below the diaphragm, is generally fatal, if not in itself, yet in consequence of the injury done to other parts. Divisions of the vagus in these situations, are associated with particular trains of symptoms, all referable to the impeded function of the organ or organs to which the nerve is distributed[523].

and calf, when the superior laryngeal nerve was irritated. On stimulating the peripheral extremities of the vagus, on the contrary, the cryco-arytenoideus posticus, and c. lateralis, were observed to contract most distinctly. The superior laryngeal nerves being divided in a young puppy, the motions of the rima glottidis were found not to be affected in the least. In a second animal of the same kind, the vagus was divided on both sides of the neck; immediately the rima glottidis closed, and never opened again, the action of the recurrents being destroyed.

[522] According to Valentin, (in Söemmerring, p. 509, and *De Funct. Nerv.*) primary fibres of the vagus also run under the inner membrane of the heart, and there minister as sensory nerves to the incessant reflex motions of the organ.

[523] More particular details may be found in Valentin. After division or paralysis of both the recurrent nerves, the following symptoms occur : the larynx becomes insensible when the injury is inflicted above the point of origin of the laryngeal branches; when it is below this point, sensation remains. In either case cough as a reflex effect from the central extremity of the nerve is apt to be troublesome; the voice is obscured, hoarse, or entirely suppressed; the sensibility of the mucous membrane of the windpipe is greatly diminished or wholly destroyed; the breathing is slower, and performed with difficulty; the arterial blood grows darker and darker, and is soon no longer to be distinguished from venous blood; the temperature of the body sinks, but rises again, at least in birds, immediately before death ; the contractions of the ventricles of the heart become weaker and quicker immediately after the division of the nerves, and continue so, until through the dyspnœa they become intermitting or slower. In the stomach the sense of hunger is annulled; but animals are apt by and by to become voracious, apparently from the sense of satiety failing; the motions of the stomach are either greatly diminished or abrogated, in consequence of which the gastric juice does not penetrate the mass of food, which in its turn is very imperfectly converted into chyme : the chemistry of the stomach, however, is not implicated, and the gastric juice shows acid reaction as usual; the power of vomiting is not affected, the act indeed often follows the operation. If the nerve be divided on one side only, or does the animal live so long as permits the two ends of the divided nerve to unite, the whole of these dangerous symptoms

The Accessory Nerve.

§ 259. The ACCESSORY, or SPINAL ACCESSORY of Willis, is generally regarded as a pure motory nerve. When it is irritated or stimulated, no indication of pain is apparent[524], but contractions in the sterno-mastoids and trapezii muscles, to which it is principally distributed, invariably follow[525]; it has farther, as it seems, a decided influence upon the motions of the heart[526]. It is still doubtful whether or not the accessory has any effect upon the motions of the larynx, or of the œsophagus and stomach. Very recent direct

may gradually disappear; death by asphyxia, however, with or without convulsions, is very apt to follow the operation.

[524] This is the inference from the experiments of Bischoff, upon the dog and goat: *De Nervi accessorii Anat. et Physiol. Com.*, p. 90; and of Valentin upon the rabbit. *De Funct. Nervor.* p. 38.

[525] Bell was of opinion that this nerve presided over the automatic respiratory motions exclusively; the voluntary respiratory motions he connected with the spinal nerves distributed to the muscles named in the text. [Bell's first paper on the nerves published in the volume of *Philosophical Transactions* for 1821, ought to be read. He is much less clear and precise, however, than might have been expected; and seems at times absolutely to abandon the principle which has since been held his highest title to distinction: viz. diversity of function in harmony with difference of origin in the nervous part, save and except with reference to what he called the symmetrical and the respiratory system of nerves. He does not once, in the whole course of this paper, allude to the influence of the two roots of the spinal nerves in conferring distinctness of office,—to the one as presiding over motion, to the other as ministering to sensation. Overlooking its origin by two orders of fibrils, he sometimes speaks of the fifth as a nerve of pure sensation, and then, but always without alluding to the cause, he refers to it as a nerve conferring voluntary motion and sensation. He had now hampered himself with a particular theory—that of a special system of nerves for the purpose of associating the most distant parts of the body in certain actions, and he will not see the conclusions that lie straight before him, and that flow legitimately from his experiments, but insists upon drawing other inferences in harmony with his views, that are utterly untenable.—For example, he says that division of the infra-orbitary branch of the fifth, paralyses voluntary motion, as well as sensation, *which it does not;* and that division of the portio dura does not paralyse voluntary motion, *which it does*, but only the movements of parts in harmony with the respiratory act, which is a pure fiction. Bell seems at this time to have forgotten his tract of 1811; he was upon a false scent; and appears only to have been brought back to the proper trail by the Experiments of Magendie, published in Aug., 1822. R. W.]

[526] Stimulation of the nerve in animals—in rabbits—is accompanied with increased action of the heart; or with restoration of the heart's action, if it have been suspended. See Volkmann, l. c. p. 498.

experiments have rendered it very doubtful whether the accessory be in fact the proper vocal nerve, as was very generally supposed at one time. The disposition now is to revert to the older idea, and to view the vagus as endowed with this office[527].

The Hypoglossal Nerve.

§ 260. The NINTH PAIR—LINGUAL OF HYPOGLOSSAL NERVE—in its mode of origin, shows the greatest affinity to the anterior or motory roots of the spinal nerves. It arises by ten or twelve distinct fasciles betwixt the pyramidal and olivary bodies of the medulla oblongata, which collect into a separate anterior and posterior bundle. Occasionally as it would seem, but very rarely, a small posterior root is observed furnished before its escape from the cranial cavity with an extremely minute ganglion[528]. In many mammalia, the posterior root would appear to enlarge regularly into a ganglion[529]; a fact which makes it anatomically probable, that the nerve in man, although more particularly comparable to the anterior root of a spinal nerve, nevertheless contains fibres which are analogous to those that proceed from the posterior aspect of the spinal chord, and are furnished with ganglions at their roots. Experiment seems to confirm the propriety of this conclusion. When the hypoglossal is divided high up in its course, little

[527] Arnold and several others inferred from pathological observations that the accessory was the vocal nerve; vide § 253 and Annot. and Arnold's *Observ. on the structure of the Brain and Spinal Chord (Bemerkungen uber den Bau des Hirns und Ruckenmarks)* Zurich, 1838, p. 123. Volkmann's more recent, and to all appearance careful, and repeated observations restore the vagus to its proper office. In his experiments on the calf, goat, dog, cat, and rabbit, just killed, he found that powerful contractions were excited in the sternomastoid and trapezius, when the accessory was stimulated, but that no motions whatever followed even in the bodies that were most susceptible of stimuli, in the soft palate, œsophagus or larynx, which on the contrary were noticed the instant the vagus was irritated. According to Valentin, the division of the accessory nerve is followed by hoarseness and aphonia, in consequence of implication of the functions of the laryngeal muscles; and simple irritation of the nerve, besides increased action of the heart, is accompanied by movements of the larynx and stomach.

[528] This ganglion was discovered by Mayer, *Nov. act. acad. Leopold.* vol. xvi. p. 744, Tab. 53.) Bach, Valentin, and others, have sought for it subsequently in vain.

[529] In the ox, hog, and dog, according to Mayer.

or no indication of pain is apparent; such expressions of suffering as have been noted, depend perhaps upon fibrils derived from other nerves, with which it gets mingled in the ganglionic plexus that is encountered on its escape from the cranium. On stimulating the posterior bundles of the hypoglossal in the rabbit, it is found that strong convulsive movements are excited in the tongue; irritation of the anterior fasciculi, on the contrary, is never followed by any thing of the kind[530].

§ 261. The hypoglossal is the motory nerve of the tongue, and guides the organ in the various operations of chewing, swallowing, and articulating so often as it comes into play in the latter act. Upon these points all observers agree[531]. When both hypoglossal nerves are divided in animals,—and the division is most easily effected in the dog—the motion of the tongue is forthwith paralysed, whilst the sense of taste and common sensibility remain. The tongue lies motionless in the bottom of the mouth, or it escapes mechanically beyond the teeth, and cannot any longer be voluntarily retracted; in chewing, it falls between the teeth, and getting lacerated, the severest suffering is occasioned, without the animal having any power to prevent the mischief[532]. In man, the motions of the tongue are frequently affected in apoplectic or hemiplegic seizures; and as a general rule, the paralysis occurs upon the side opposite to that on which the general attack has fallen. It would appear that the descending branch, (descendens noni,) which is commonly spoken of as furnished by the hypoglossal, receives but

[530] Valentin (Söemmerring, p. 524) says, that on dividing the nerve in the dog and horse, high up, towards the anterior condyloid foramen of the occipital bone, little or no evidence of pain is afforded. The indications of suffering which Magendie and Desmoulins, Mayo, Steinrück, and others, observed, were possibly caused by implication of certain commingled fibres of the pneumogastric and superior cervical nerves. Valentin performed the experiment on the rabbit, *De Funct. Nerv.* p. 39. That the nerve is principally motory is the conclusion of all observers, from Magendie to Jo. Müller, Valentin and Volkmann; under the influence of mechanical or galvanic stimulation, the most powerful convulsions are aroused in the tongue from its root to its tip.

[531] Galen appears to have regarded the hypoglossal as the motory nerve of the tongue; it was Boerhaave who in modern times first upheld it as the gustatory nerve. The experiments of Magendie, Mayo, Müller, Panizza, Gurlt, Kornfeldt, Valentin, Volkmann, and others, all agree in demonstrating the hypoglossal as the exclusive motory nerve of the tongue.

[532] See Panizza, Functions of the nerves, and Valentin, l. c., on this point particularly.

very few motory fibres from this nerve, inasmuch as the thyro-hyoideus alone, more rarely the sterno-hyoideus, is thrown into convulsions upon the galvanic stimulation of the nerve; none of the other muscles upon which the branch is distributed are affected[533].

Of the Functions of the Spinal Nerves.

§ 262. When the posterior roots of the spinal nerves which supply the hind leg of a frog are stimulated, we perceive no trace of convulsive or other movement in the limb; but if we apply our means of stimulation or irritation to one or more of the anterior roots, convulsive twitches and contractions of one or more of the muscles are forthwith induced. If the posterior roots on the right side be now divided, the right leg is rendered insensible; it may be pinched, cut, burned, etc., without the animal giving any indication of suffering pain. If the posterior roots be left untouched, and the anterior roots be cut through, the creature is rendered incapable of moving its limb; which, however, is not deprived of sensation, for the creature gives evidence of suffering pain when the extremity is injured in any way,—it endeavours to escape, dragging the now motionless part behind it[534]. In making this experiment, it is only necessary not to use galvanism of too great intensity; for if this be done, the stimulus is communicated from one root to another,—motion fol-

[533] Volkmann found, on a microscopic examination of the descendens hypoglossi, that the fibres have not all a course towards the centre, but have obviously a peripheral origin to a considerable extent; it appears that the fibres are derived from the superior cervical pairs; physiological experiments confirm this idea. [If the descendens noni be traced to its connexion with the lingual nerve, and examined with care, it will be found to be formed by two filaments, one from the lingual, the other of larger size, from the first and second cervical nerves. Wilson's *Anatomist's Vade-Mecum*, p. 374. R. W.]

[534] Frogs are the best subjects for demonstrating the difference of function of the anterior and posterior roots of the spinal nerves; they were first used for this purpose, and with the most decisive results, by Müller. Mammalia are much less eligible: the operation of exposing the spinal chord in them, is a most barbarous procedure, and is always attended with serious loss of blood; [the fall of temperature that ensues is also an important consideration,] and the results that have been obtained from them are not always so decisive; those of Desmoulins and Magendie left nothing but doubt; Panizza appears to have been more successful. The spinal canal may either be laid open through its entire length, or the upper or lower portion only exposed. The different roots are to be carefully raised with the needle already described, (§ 243,) and divided

lows when the posterior roots are operated on, and indications of pain ensue when the anterior are irritated: the galvanic fluid of any intensity is conducted from one moist part to another, and a universal instead of a merely partial excitement is the consequence. This is doubtless the source of the discrepancies that are observable in the results of different experiments[535]. It is also very necessary not to be deceived by reflex actions, which are produced when stimuli are applied if the roots of the nerves be still in connexion with the spinal chord. In this case, the irritation is apt to be transferred from the sensory roots to the spinal chord and brain, and from thence to extend to the motory parts, when of course spasms and convulsive movements follow. The law in regard to the function of the anterior and posterior roots of the nerves arising from the spinal chord, as laid down by Bell, has hitherto only been confirmed by every carefully performed experiment[536].

§ 263. In man, and all vertebrate animals, the posterior roots of the spinal nerves are furnished with ganglia, over which the primary fasciculi of the anterior roots pass without mixing. Immediately beyond the ganglia, the primary bundles of the anterior and posterior roots blend together, and form common trunks, which as being of mixed nature themselves, send off branches and twigs of mixed nature also, which penetrate to all parts of the body, fasciculi being supplied to the great sympathetic, to the muscles, and to the skin. The principal masses of the spinal nerves are sensitive; but they all contain a larger or smaller number of motory fibres; even the branches supplied to the skin are in this predica-

close to the spinal chord; the roots are then to be laid upon a narrow strip of thin glass, and stimulated mechanically, or with the simple pair of pointed galvanic plates. Some little practice and dexterity are of course necessary to lay bare the chord nicely; but with the bent scissors, or the cutting pliers, (§ 243,) it may be exposed in the frog without much difficulty.

[535] Seubert was misled in this way; instead of a single pair, he operated with fifty pairs of plates! (*De Functione Rad. Ant. et Post. Nerv.*, 1833,) and the notice of the dissertation by Müller in his Elements.

[536] Volkmann in his generally excellent dissertation, already so frequently quoted, appears to have come back to the original idea of [Bell and] Magendie, viz: that the posterior roots are not exclusively, although principally, sensorial; and the anterior in like manner, whilst they are mainly motory, are not exclusively so. He particularly quotes an observation of Dr. Marshall Hall, who saw movements excited by stimulating the posterior roots of the spinal nerves, in a tortoise and a skate. These motions Müller refers with propriety to reflex movements. *Archiv f. Physiol.* 1840, S. 509.

ment, as is made obvious by the shrinking and corrugation of the integuments that constitutes goose-skin; and the muscles, as they possess sensibility, although in a moderate degree, so must they have a few sensitive fibres distributed through their masses. The superior cervical nerves farther enter into combinations with several of the cerebral nerves; their sensitive fibres go to the integuments of the occiput, ear, chin, and cheek; and they send motory fibres to several of the muscles of the tongue[537]. The phrenic nerve is principally made up of the rudimentary fibres of the fourth cervical nerve, though it receives additions from the second, third, fifth, and seventh cervical pairs, as also from the glosso-pharyngeal, and in all likelihood also from the vagus. The phrenic is evidently made up of bundles from both roots of the cervical nerves, and therefore contains sensitive fibres; but it is far more a nerve of motion than of sensation; it is distributed almost exclusively to the diaphragm. When the trunk of the nerve is stimulated in the chest, strong spasms of the whole anterior expansion of the diaphragm are excited[538]. The phrenic is the nerve of the involuntary respiratory movements that are effected by the rising and falling of the diaphragm. But it would seem that both of the phrenic nerves may be divided in animals without any apparent immediate or more remote detriment to life[539].

Of the Functions of the Great Sympathetic.

§ 264. In regard to the sympathetic nerve, and its functions, two mutually opposed views are at the present time entertained by physiologists. One party, and this has hitherto been the predominating one, considers the sympathetic as a distinct nervous system, independent, to a certain extent, of the brain and spinal chord, and

[537] The experiments of Volkmann (l. c. 504) have shown, that on irritating the superior cervical nerves, muscles were thrown into contractions which either seemed to depend wholly on these nerves, such as the sterno-hyoideus, sterno-thyroideus, and others, or on the eleventh and twelfth pairs also, such as the thyro-hyoideus, the sterno-mastoidus, and various others of the neck.

[538] This is one of the simplest experiments in rabbits and dogs particularly, and the nerve often retains its irritability for something like an hour after death. I have not, any more than Valentin, observed motions in the stomach and heart to be occasioned by irritations of the phrenic nerve.

[539] This at least is the case in rabbits, according to Valentin's experience: *De Funct. Nerv.*, 60.

comprises it under the special designation of the ORGANIC NERVOUS SYSTEM[540]. Besides its connections with the brain and spinal nerves, from which it receives fasciculi, it is held to include peculiar organic fibres, the existence of which, however, as already stated, (§ 233 and Annot.) is problematical. The sympathetic appears much rather to comprise no peculiar or intrinsic fibres. The gray aspect of particular bundles depends on an admixture of ganglionic matter with their fibrils; the dirty reddish hue of other nerves is connected with the presence of an unusual quantity of highly vascular filamentous tissue, which often surrounds single primary fibres abundantly. We have, in fact, no evidence of the existence of any other than the ordinary motory and sensitive fibres in the sympathetic, these being derived from the other cerebral and spinal nerves, and being plentifully surrounded in the different ganglia of the head, neck, thorax, and abdomen, with ganglionic globules or cells. The primary fibres seem at most only to become somewhat thinner in the ganglions than they are beyond them, (§ 231.) In this view, consequently, the sympathetic nerve is virtually a cerebro-spinal nerve, and such is the light in which it now begins to be very generally regarded[541].

§ 265. From recent investigations, it appears certain that the sympathetic receives twigs from the whole of the cerebral nerves, except those of the three higher special senses—smell, sight, hearing; and farther, from both the anterior and posterior roots of the spinal nerves at large[542]. The primitive fibrils of the sympathetic form plexuses within its numerous ganglia, and have numerous ganglionic corpuscles interposed between them. They

[540] The idea of the sympathetic being a distinct nerve, was originally broached by Söemmerring: "it is a nerve that exists independently, and is only connected with the cerebral and spinal nerves." On the brain and nerves (*Lehre vom Hirn und Nerven*), 2d ed., 1800, p. 322. Bichat, again, is the originator of the doctrine of an organic system of nerves. The old anatomists considered the sympathetic now with Haller as a cerebral nerve, now with Petit as a spinal nerve. See Valentin, *De Funct. Nervorum.*

[541] Valentin in particular is the decided advocate of this simple mode of regarding the sympathetic. Vide § 233.

[542] The connections with the cerebral nerves appear to be especially effected by the medium of the ganglia of the oculomotor, trigeminus, facialis, glosso-pharyngeus, accessorius, and hypoglossus; in other words—the ciliary, otic, sphenopalatine, petrous, cavernous, and inferior maxillary ganglions. Fibrils have been detected proceeding from it to all the cerebral nerves save the trochlearis.

emerge unchanged from the ganglia,[543] from which no new or particular fibrils appear to originate.

§ 266. Comparative anatomy brings many arguments in favour of the view, that the sympathetic is nothing more than a cerebro-spinal nerve. In the cyclostomes among fishes, the sympathetic is either wholly or in major part replaced by the par vagum ; the same thing occurs among serpents, in which, moreover, branches proceed directly from the spinal cord to the viscera. It is a remarkable anatomical fact also, that in man and the mammalia, the lachrymal gland and several other organs of secretion, such as the mamma, are supplied with nerves directly from the cerebro-spinal system, not mediately from the sympathetic[544].

§ 267. The nerves which the sympathetic supplies to the viscera, are the instruments of their sensations and motions. It is, for example, easy to demonstrate by experiment, that the peristaltic motions of the intestines in the rabbit, dog, and other animals, is powerfully and permanently increased by the stimulation of the solar plexus, or of any particular branch proceeding directly to the intestines[545]. By other experiments of the same kind, the motory

[543] It was already observed in the last paragraph, that the primitive fibrils appeared generally to be somewhat thinner, as if they had become compressed between the ganglionic cells, a circumstance which would render an anatomical or simple physical reason for the influence of these minute corpuscles upon the nervous fibrils.

[544] [As knowledge extends it becomes more simple and less burthensome to the memory. Well might M. Pibrac say : "Si nous etions debarassés de tous nos erreurs, nous perdrions une grande partie de notre savoir,"—a sentence which Mr. Abernethy used to paraphrase thus : "Increase of knowledge, unlike other growth, is often attended with a shrinking in the mass." We have heard a good deal about the derangements of the ganglionic system of nerves in discussing diseases of late years ; it is to be hoped that this piece of scientific mystification will now come to an end. R. W.]

[545] This is one of the most easily performed experiments, and was originally imagined by Jo. Müller. The abdomen of a rabbit just killed, is opened as quickly as possible. After a few seconds, apparently from the stimulating effects of the external air, peristaltic motions of considerable energy begin, but they soon fall off in force, and by and by cease entirely. If upon this the cœliac ganglion be touched with a solution of caustic potash, powerful vermicular motions of the intestine commence forthwith ; similar motions can be excited in any particular loop of intestine, by operating on the principal nerve which supplies it. That these are not reflex movements only, is evident from their taking place when the piece of intestine with its mesentery is removed, and the stimulus is applied to the nervous branches.

power of other fibres, and their influence upon the viscera, can also be shown[546]: the heart is excited by stimuli applied to the inferior cervical ganglion, and also, but in a much inferior degree, by irritating the superior thoracic ganglion[547]. It has even been said that the great vascular trunks of the thorax and abdomen have been seen to contract under the influence of stimuli applied to the thoracic ganglia[548]. Stimulation of the cervical ganglia induces contractions in the œsophagus; and movements of the stomach follow excitement of the four inferior cervical pairs and of the two superior thoracic ganglia. Many branches of the sympathetic and other nerves minister to the motions of the small intestines[549]. Stimulation of the lower lumbar and superior sacral nerves is followed by powerful contractions of the great intestines, urinary bladder, uterus, and oviduct. The greater splanchnic nerve having been stimulated in the horse, the ductus choledochus communis has been seen to contract, and in birds this fact is easily demonstrated, and very remarkable. In the same way, motions have been observed in the ureters, on applying stimuli to the abdominal ganglia, and to the roots of the abdominal spinal nerves. The bladder receives its nerves principally from the sacral portion of the

[546] The very satisfactory and numerous experiments of Valentin demonstrate this,—*De Funct. Nerv.* He repeated them on the carcases of upwards of 300 horses, rabbits, and sheep; but rarely on those of dogs and cats, as in them the susceptibility to stimuli speedily ceases.

[547] The heart, moreover, Valentin reports to have been powerfully moved on stimulating the cardiac plexus, the roots of the accessory, and four first cervical nerves, and the trunk of the vagus betwixt the larynx and thorax; the greater number of the motory fibrils received by the heart, appear to be derived from the vagus.

[548] It is more difficult, Valentin says, to make sure of the contractions of the great vascular trunks; the aorta of the horse diminishes in size, however, when the thoracic ganglia from the third onwards are stimulated. The veins contract more remarkably but more slowly than the arteries; Valentin observed the vena cava abdominalis to be drawn together when the sympathetic of the abdominal cavity was irritated; he also noticed the thoracic duct to contract when the thoracic portion of the nerve was stimulated.

[549] Valentin observed increased motion of the small intestines when the oculomotor in the cat and horse was irritated; no such effect followed under the same circumstances in the rabbit and dog. In animals generally, excitement of the roots of the trigeminus and accessory, and of the dorsal and lumbar nerves, was followed by increased movement in the intestinal tract.

sympathetic; the vas deferens and vesiculæ seminales, contract upon the two inferior lumbar ganglia being stimulated[550].

§ 268. The sensibility of the parts to which the sympathetic sends branches, is for the major part moderate. Wounds of such parts are accompanied at the moment with little or no pain. But many pathological phenomena, for example, inflammations of the abdominal viscera, neuralgiæ of the same parts, the contractions of the uterus during parturition, and of the bowels when they contain flatus or some undigested matter, mechanical irritations, such as stones lodging in the pelvis of the kidney, or in the bladder, or passing down the ureters, etc., give us ample assurance that the sensibility upon occasion may reach a high pitch of intensity. Direct experiments upon animals show similar phenomena. Even when slight mechanical or chemical stimuli seem to produce no pain, animals nevertheless cry out lustily when more powerful means of irritation are resorted to, such as caustic alkali, smart pinching, the application of ligatures, etc. It would appear, too, that a ganglion becomes always the more painful the longer it is exposed to the air; and farther, that fibrils which proceed from gangliform plexuses, are not affected by slight stimuli so readily as those that enter them[551].

§ 269. If we agree, then, that the sympathetic in general performs the functions of the cerebro-spinal nerves at large, we must still admit that it exhibits numerous peculiarities. It not only extends over all the vegetative organs of the abdomen, and in part also of the thorax, but by its fibrils detached from the ganglia, it accompanies the great blood-vessels in their course, and with these penetrates every part of the body. In its motory as well as in its sensitive functions, it also exhibits essential modifications: the motions of the parts to which it is distributed are abstracted from the empire of the will. These involuntary, and in the healthy state unconscious, motions extend to the most remote structures with which it is in communication, by means of ganglia, such as the iris, for example. Reaction upon stimulation generally lasts longer than the stimulus, which is exactly the reverse of what happens in reference to the muscles of voluntary motion, when the reaction so

[550] The data so far are derived from Valentin, to whom we are indebted for by much the most extensive and accurate series of experiments that has ever been performed on the points referred to.

[551] Vide Valentin, *De Funct. Nerv.* p. 70.

constantly ceases before the stimulus is removed. The sensibility, as already observed, is extremely slight in the healthy state. The conduction from the peripheral to the central parts, has therefore undergone a manifest alteration, and even partial interruption, as it would seem. The central parts receive no impressions from the organs which are supplied with nerves from the sympathetic; and they have, farther, no power of controlling the motions of these organs. These remarkable effects can only be referred to the influence of the ganglions.

Retrospect of the Functions of the Nerves.

§ 270. When we survey the functions of the several nerves in their connections, and with an eye to their anatomical origin and peripheral distribution, we perceive certain general characters, which are referable to a small number of capital divisions. 1*st*, The three nerves of special and higher sense differ in structure, origin, evolution, distribution, and function, from all the rest[552]. 2*d*, It appears that all the cerebral nerves, with the exception of these three, consist of intermingled motory and sensitive fibrils. 3*d*, The common cerebral nerves unite in part with the nerves of special sense as complementary to them, and supply them or the organs on which they are distributed with sensation and motion. 4*th*, The cerebral nerves also comprise fibrils endowed with what may be called special senses—certain kinds of taste, hunger, thirst, [the necessity of taking breath,] etc.; or the general sensibility is manifested by them with peculiar delicacy and acuteness (the fifth pair.) 5*th*, The several cerebral pairs distribute their motory fibrils to particular muscles, or groups of muscles, the voluntary or automatic motions of which they controul. As a general rule, too, every muscle of the head derives its motory power from one, not from two cerebral nerves. The muscles of the eye seem, however, to form an exception to this rule[553]. 6*th*, The prototype of the mode

[552] The chapter on the more intimate structure of the nerves and organs of sense may here be referred to again.

[553] This particularly appears from Volkmann's researches. Several muscles of the tongue (and the iris) receive motory fibres from nerves of the spinal chord as well as from nerves of the brain, which renders the implication of the speech, so common in affections of the spinal chord, more comprehensible. Vide Volkmann, in Müller's *Archiv*, 1840, S. 508.

of origin of the cerebral nerves by distinct roots, exists in the spinal nerves, in which double roots, having different functions, one set furnished with a ganglion, the other not so furnished, are regularly observed; in the cerebral nerves the mode of origin by a two-fold set of roots, and the existence of a ganglion, are to be traced with greater or less distinctness in reference to different nerves; sometimes they are merely indicated. 7*th*, The sympathetic derives its motory and sensitive fibrils from the cerebral and spinal nerves; its function, however, is peculiarly modified, sometimes contracted, if the term may be used, by the influence apparently of the ganglionic corpuscles. 8*th*, The more anteriorly the nerves arise, the more they are connected with the cerebrum, the greater is the proportion of special sensitive fibrils which they contain, the more truly cerebral is their structure, circumstances that are particularly apparent in the first and second pairs.

SECTION THE SECOND.

OF THE SENSES.

Of the Senses in General.

§ 271. From the general peripheral nervous system, as the agent or medium of common sensation, certain individual portions are fashioned into organs of special sensation, which make us acquainted either with the state of our body, and with the existence and qualities of objects beyond us; in other words, they establish relations between the brain as the central organ of perception, and the material universe and its properties. By means of these organs we acquire those specific sensations, or capacities of being peculiarly impressed, which we designate TOUCH, TASTE, SMELL, HEARING, and SIGHT. Certain nerves are susceptible of these specific sensations only, and these we name particularly NERVES OF SENSE. Their nature has already been discussed in a general way, (§ 244.) Here I propose to speak of them more at length.

We cannot say that we perceive the sensible qualities of things, such as colour, sound, etc., as such; we are only aware, by our consciousness or percipient part, of the specific excitement of the nerve of sense that has been occasioned by the external force with which it is in relation. The same thing is true likewise of the internal organic excitements. But certain classes of the qualities of matter stand in a specific relationship to particular nerves, affect them most powerfully, and occasion diversified phenomena; whilst other qualities, again, only act as stimuli in general, and give rise to more or less limited reactions in particular nerves in the direction of their appropriate energies. Such a quality, for example, is light in reference to the eye, which is admirably organized for the perception and discrimination of luminous undulations of all kinds; but the optic nerve when stimulated in any other way,—by pressure, galvanism, etc., still experiences a subjective impression of light, not any impression of pain, such as is excited in an ordinary sensitive nerve, or any spasm, such as takes place in the muscle to which a motory nerve is distributed[554].

§ 272. We divide the senses into simple and compound; the simple senses are—TOUCH, TASTE, SMELL. We have no special physical apparatus formed upon or connected with the nerves of any of these senses; their nerves penetrate the tissues, like the generality of the nerves, and seem to undergo very unimportant alterations in the peripheral expansions of their primitive fibrillæ. These, however, lie very superficially, and are only covered with very thin epidermic or epithelial laminæ, by which the impressions of external agencies are enabled to reach them with the least impediment. The compound senses are SIGHT and HEARING; associated with the nerves of which we have apparatuses of great perfection, and delicacy of structure, perfectly adapted to receive and communicate the physical qualities with which they are in relation, in all their varied forms[555].

[554] The general physiology of the senses, their relations to the soul as well as to the external world, the questions of the internal nature of the subjective sensations to the physical qualities, will first become appreciable after we have analysed the individual phenomena of sense, and the functions of the central parts. We defer these considerations, therefore, till we come to the General Physiology, where the history and critical review of the various opinions upon the subject will also very appropriately find a place.

[555] In the following paragraphs we shall analyse the phenomena of the individual senses, commencing with the most simple, and taking as frequent occasion

CHAPTER I.

OF THE THREE SIMPLE SENSES.

Of Touch.

§ 273. Common sensation makes us acquainted with the form, temperature, weight, and cohesion of bodies,—it is the sense that is in relation with the mechanical conditions of things and with temperature. The capacity to recognize external impressions inherent in all the nerves of common sensation, is exalted into TOUCH in particular situations, its acuteness being greatly influenced by the mode of distribution of the nerves, and the nature of the tissue in which it takes place. Tissues which have few nerves, and these of small size, such as the cornea, the teeth, etc., are without sensation, or they seem to have sensation only in consequence of conducting the stimuli which act on them to other neighbouring parts[556]. All other parts of the body besides are susceptible of mechanical, chemical, and other kinds of stimuli. Tendons, cartilages, and bones which only receive nerves from those branches of the sympathetic that accompany the blood-vessels, possess sensibility in the lowest degree; these parts, however, as is well known, become possessed of very acute sensibility under certain circumstances, when they are affected with inflammation, for example, like all the other organs supplied by the great sympathetic [557]. The muscles, too, have but little sensibility: a condition which depends on the

as possible to refer to the mutual influence of the several senses. A very complete literature of the organs of sense may be found in the works of Treviranus, particularly the sixth volume of his *Biology*, and his *Phenomena and Laws of Organic Life*, vol. ii, and also in the Elements of Rudolphi, Müller, Magendie, and Arnold. Among plates, the well known ones of Söemmerring, and the recently published very admirable *Icones Anatomicæ* of Arnold, Fasc. ii. are the best.

[556] A well known unpleasant sensation is what is called the setting on edge of the teeth under the influence of acids; the impression, however, is not perceived by the enamel of the teeth, but is conducted by this, to the nerves of the pulp, which are derived as we have seen from the fifth pair.

[557] Haller long ago demonstrated the insensibility of the healthy bones and tendons, to wounds and injuries, by experiments on man and animals.—vide *Commentar. Gottingenses*, T. ii, 1752, and *Element. Physiolog.*, T. iv, p. 276.

sparing admixture of sensitive with their numerous motory fibrils, although it would appear that all, even the most purely muscular nerves, such as those of the eye, have sensitive fibrils in small numbers mingled with them, (§ 248-250.) In attacks of cramp in the calf of the leg and other parts, we are made aware that inordinate or abnormal contractions of the muscular fibre may be accompanied with very severe suffering; and on the other hand, the rhythmical contractions of the ejaculatory muscles are attended by pleasurable sensations of the most peculiar and intense description, (§ 37.) The most sensitive parts, however, after the general external surface, are the mucous membranes at large,—of the nose and mouth, of the air-passages, intestines, and urethra.

§ 274. Of all the senses, touch is the most extensively diffused throughout the animal kingdom[558]. Even among the invertebrata we observe certain organs, plentifully supplied with nerves, which serve as true organs of touch, and which in the annellidans, molluscs, crustaceans, arachnidans, and insects are designated as tentacula, palpi, antennæ, etc. Among vertebrata, again, where the skin, from fishes onwards to the very highest mammals, is so constantly covered with horny or epidermic structures in the shape of scales, feathers, and hair, and where the extremities of the toes are occupied by nails, claws, and hooves, the fifth appears to take the lead, and often to stand exclusively as the nerve of touch. The lips, nose, and snout or proboscis, and the strong hairs that so frequently grow from the upper lip and corners of the mouth, are all plentifully supplied with nerves from the infra-orbitory branch of the fifth, and serve the lower animals as special organs of touch[559]. In all the soft-billed water birds, as in the duck and snipe tribes, large branches derived from the fifth are ramified under the soft skin of the beak; the same thing occurs in regard to the beard or processes about the mouths of fishes. In cases where the point of the tongue serves for an organ of touch and prehension, as it does in many amphibia and in mammals, the faculty of touch is conferred by the fifth pair.

[558] It would seem that even the infusoria—the vorticellæ in particular, and the polypes possess the sense of touch, although hitherto no one has discovered the nervous system of these creatures.

[559] For many interesting details, see the work of Rapp, on the functions of the fifth pair, (*Die Verrichtung des Fünften Nervenpaares*, Leipz. 1832).

§ 275. In man the power of perceiving tactile impressions is extremely different in different parts of the surface, a circumstance which, though it may in some measure depend on the extent of nervous endowment, and partly on the thickness or thinness of the cuticular covering, is probably in more immediate relationship with the specific susceptibility of the nervous fibrils distributed to particular spots[560]. With the exception of the nerves of the three higher senses, however, the whole of the spinal and cerebral nerves comprise fibrils that are susceptible of the ordinary tactile impressions. In the lips, the tip of the tongue, and the palmar aspect of the last joint of the fingers, the nerves are both very numerous and superficially distributed, and whilst the epidermic layer is thinner, there is at the same time a greater degree of isolation of the papillæ of the skin, between lines and furrows of the epidermis. The tactile papillæ are small conical projections of about half a line in diameter, situated betwixt the cuticle and the more compact fibrous layer composing the corium. They consist principally of convolutions of vessels and nervous loopings; by their bases they appear connected, but they are still divided by furrows and lines, and transpierced by the canals of the deeper lying sudoriparous glands, (Fig. CLXXXIX.) The primitive fibrils of the nerves are not so simple in their peripheral terminal loopings here, as they are generally (§ 232); for each primitive fibril in forming a loop is at the same time convoluted into a little ball. A vast number of such balls are often found arranged rosette-wise and in lines, with the obvious effect of extending the surface displayed by the primitive fibrils, and so multiplying the points of contact[561].

§ 276. Various experiments may be tried to prove the greater or less susceptibility to impressions of different parts of the skin under different circumstances. The impression is always stronger as the surface exposed to it is greater, a fact which may at once be ascertained by plunging a single finger of one hand and the whole of the

[560] Arnold has given good delineations of the tactile papillæ in his *Icones Anatomicæ*, Fasc. ii. Tab. xii.

[561] This interesting relation of the convoluted terminal loops of the nerves of the skin, which bear the closest resemblance to the glomeruli of blood-vessels, was first described by Gerber. Vide his *General Anatomy*. Gerber recommends us to steep the slices of cutis that are intended for examination in oil of turpentine, before placing them under the microscope, a mode of preparation which makes the nerves milk-white.

other hand into water, either of a higher or lower temperature than that of the body[562]. Double or multiplied impressions, also, always occasion double or multiplied perceptions in the mind,—we have a perception in reference to each half of the body, and to every finger that grasps an object. The following general phenomena are recognised when the perception of tactile impressions by the skin is analysed: the skin moistened feels less acutely than it does when dry[563]; warmth in general augments the susceptibility of the skin; cold, on the contrary, lessens it[564]. Acids applied to the skin at first increase the keenness of touch; but they afterwards diminish it. Narcotic substances, when by imbibition they are brought into contact with the nerves, blunt the acuteness of touch.

§ 277. The experiments by which the degree of tactile susceptibility possessed by different parts of the skin may be proved, are interesting and easily repeated. It is only necessary to take a pair of compasses and to approximate or separate the points until the mind loses or acquires the consciousness of a double impression. When the tip of the tongue is tried, the double impression is distinct when the points are not more than half a line apart; whilst in the skin covering the upper part of the arm, the thigh, and the middle of the back, the points must be separated thirty lines before the mind becomes aware of a double impression[565]. In the ex-

[562] See on this topic the important conclusions of Weber, contained in his work entitled: *De Pulsu, Respiratione Auditu et Tactu Annotationes*, 4to, Lips., 1834. The experiments referred to were repeated and confirmed by Thomson, Valentin, and myself. Valentin has given some interesting additions in his tract: *De Nerv. Funct.*, p. 118, &c.

[563] On this and the following phenomena, see Valentin, *Op. Cit.*, p. 121.

[564] This seems to depend principally upon the locally increased or diminished afflux of blood.

[565] See the interesting table of Weber in the work above quoted, and in Müller's *Archiv*, 1835, p. 154. Dr. Allen Thomson in *Edinb. Med. and Surg. Journ.*, No. 116. The separation of the compass-points to produce two impressions, was as under: on the tip of the finger 1 line; on the red part of the lip 2 lines; on the palmar aspect of the second joint of the finger 2, and on the opposite aspect 3 lines; on the tip of the nose 3 lines; on the dorsum of the tongue and skin of the lips 4 lines; on the point of the great toe, on the cheek, back of the second joint of the finger, and middle of the palm 5 lines; on the hard palate 6 lines; over the zygoma 7 lines; on the back of the wrist 8 lines; on the inner aspect of the lips 9 lines; on the forehead 10 lines; on the occiput 12 lines; on the back of the hand 14 lines; on the neck under the chin 15 lines; over the patella and in its neighbourhood 16 lines; over the sacrum 18 lines; on the sternum 18

tremities the double impression is more easily detected when the points are applied transversely than lengthwise[566]. The delicacy of touch, as of all other kinds of nervous impressibility, is much greater in some individuals than in others; it may be twice as delicate in one as in another[567]. In a general way it may be said that the fineness of touch in the most sensible parts, such as the tip of the tongue, is from fifty to sixty times greater than in the least sensible parts, such as the back and limbs. Instead of using compasses, analogous experiments may be tried on ourselves and others by means of weights, these being placed upon different parts, and the impressions compared. The results are the same. Weights, however, must be judged of by the nerves of the skin and muscles acting simultaneously[568].

§ 278. Touch, like all the other senses, can be improved and rendered more acute by exercise or education[569]. When we would particularly inform ourselves in regard to tactile impressions, we fix our attention firmly upon the object examined, and at the same time make various movements in order to bring the greatest possible number of cutaneous papillæ into contact with it. This examination with attention, accompanied by muscular movements,

lines; over the lumbar vertebræ 24 lines; over the middle of the humerus and of the thigh, and also in the middle of the back according to Valentin, 30 lines.

566 Valentin, l. c. p. 120.

567 As appears from the experiments of Valentin, who experimented on himself and five other persons.

568 To distinguish between the impression made upon the integument and that made upon the muscles by the imposition of weights, Weber experimented under circumstances in which the hand upon which the weights were placed was perfectly supported by a cushion upon which it rested. In this way, the muscles being altogether passive, the discrimination was much more nice than when the common sensibility of the muscles was at the same time called into play. In the same places where the sensibility was found to be greatest by the compasses, was it also found that the sensibility to impressions of weight and of temperature was greatest. For example, to have the same idea of pressure from a weight laid upon the point of the finger and upon the forehead, the weight upon the forehead must be from a quarter to a third heavier than that upon the finger. Weber, l. c.

569 This appears particularly in nations of slender make and having very fine skins. The female silk throwsters in Bengal, according to Ritter, will distinguish by the touch alone 20 different degrees of fineness in the unwound cocoons, which are sorted accordingly with the greatest precision: the hand of the Indian muslin weaver is so delicate that he contrives to make the finest cambric in a loom of such simple construction that European fingers could at the best propose to make a piece of canvass in it. See my *Natural History of Man*, vol. 2, p. 118.

we particularly designate FEELING or TOUCHING. Mental consciousness is always divided in the course of touching; the character of the impression therefore depends in part at least upon habit, and we are extremely liable to be deceived when we exercise the sense of touch in any unusual way[570]. Secondary impressions, as in the case of all the other senses, are also very apt to remain behind: we still fancy we wear the ring to which we have been long accustomed, though we have laid it aside, etc.[571]. So likewise have we subjective sensations independently of external stimuli,—for example, feelings of cold and of heat in diseases, without any peculiar depression or elevation of the external temperature, etc. These subjective sensations are, however, mostly connected with internal organic excitements, to which idiopathic pain likewise belongs, and are not so different from objective or external impressions as is generally supposed[572].

Of Taste.

§ 279. The tongue is the organ of taste: it is extremely doubtful whether any other part in the mouth perceives the sapid qualities of bodies, although some physiologists have maintained that the palate possesses taste in common with the tongue[573]. The extent

[570] The familiar instance in which a pea or other small rounded body is felt as if it were double, when it is touched by two fingers of the same hand crossed, will serve as an illustration.

[571] This may be ascribed to *memory* in the senses, to which also the feeling of entireness or integrity in the common sensation must be attributed,—that feeling which leads one who has had a limb amputated, still occasionally to complain of feeling pain or uneasiness in the fingers or toes of the lost member.

[572] In inflammations and fevers, the temperature does in fact rise locally or generally, and the internal stimuli that give occasion to pains, are in many cases virtually referable to the class of mechanical irritants.

[573] From a series of experiments undertaken on myself and two other persons, I concluded that neither in the palate nor in any other part of the mouth—always excepting the tongue—was there any perception of taste. Both older and more recent observers differ from this conclusion. Blumenbach (*Comp. Anat.*, 3rd ed., p. 337,) instituted experiments on a man born without any tongue. This man having his eyes bandaged, always recognised solutions of bitter and of various saline substances. But we are not sufficiently informed as to the state of the root of the tongue in this case, a part where the perception of taste is extremely keen, and which so commonly exists even in cases of congenital deficiency of the rest of the organ. Many cases of the kind will be found referred to in Rudolphi's *Physiology*, ii. p. 91. Rudolphi is himself, as I conceive, opposed to the idea, that

to which the sense of taste is distributed over the tongue,—whether it inheres in the entire organ, or is confined to the tip or to the root; whether the specific sensation for different substances is the same or different in every part of the member, etc.;—upon these points very opposite opinions have been maintained, in spite of the ease with which the whole subject might apparently be passed in review, and definite conclusions obtained. The question at large is most intimately connected with the one in regard to the nerve which is actually the instrument of taste. Of the three nerves which are distributed to the tongue, the hypoglossal is now universally admitted to be the nerve of motion; but then some recognise the glosso-pharyngeal, and others the lingual branch of the fifth, as the proper nerve of taste; and others, again, regard the two nerves as essential to the perception of the sapid properties of bodies; each party of course appeals to anatomical and physiological facts, to experiments upon animals, and to personal observation, in support of its views[574].

§ 280. Comparative anatomy supplies us with a few data upon the subject of taste, although probably with none that will stand the test of severe criticism. It would be important were it confirmed that in birds the tongue either received branches from the glosso-pharyngeal alone, or from this and the par vagum, but not

any other part than the tongue is ever an organ of taste. Magendie (*Physiology, sub Capit.*) however is of opinion that the specific sensibility extends over the teeth, the gums, the palate, and the pharynx. He dwells particularly upon the experiments of Guyat and Admirault, according to whom, there is a small spot on the soft palate, between its attachment to the palatine bones and the uvula, which possesses taste in a very distinct manner. In my own experiments I observed nothing of the kind. Valentin has mentioned many interesting facts in connexion with this subject, (*De Funct. Nerv.*, p. 116). In no instance did the hard palate appear to possess any sense of taste; among eight individuals, the soft palate and uvula seemed distinctly gifted with a sense of taste in two; in four, the perception of flavour here was much less distinct; and in two, it was entirely absent. The anterior arch of the palate and the posterior aspect of the uvula, tasted decidedly in two persons, in one less distinctly, and in three either not at all or very indistinctly. The posterior arch of the palate, the tonsils, and the surface around the epiglottis, seemed in every case to possess perceptions of flavour.

[574] See § 254; Panizza's *Ricerche Sperimentali*, Valentin's *De Funct. Nerv.* p. 44 and 116, and my observations in Froriep's *Neue Notizen*, No. 75. W. Horn, *On the Human Taste,—Ueber den Geschmacksinn des Menschen*, Heidelb. 1825, also made many experiments on taste in different places, and upon the different effects of sapid bodies.

any from the trigeminus, the lingual branch of which seems to be entirely wanting in this class[575]. In man and the mammalia the glosso-pharyngeal is distributed to the papillæ circumvallatæ, parts which in different orders and species exhibit numerous varieties in point of form, number and position. It is also remarkable that the tongue should be covered in so many animals upon its point and anterior upper part with spines and a layer of epithelium of unusual thickness and hardness,—an arrangement which is evidently little favourable to great delicacy of taste, whilst as a general rule its base is thickly studded with soft papillæ—gustatory papillæ, of various form and magnitude[576].

§ 281. Experiments upon animals have shown that when the hypoglossal or ninth nerve is divided, the motions of the tongue in the great majority of instances are completely annulled, whilst the sense of taste and the common sensibility remain entire (vide § 254.) The conclusions of different observers differ somewhat as to the consequences of dividing the glosso-pharyngeal; one constant effect, however, appears to be the loss of taste. When the lingual branch of the fifth pair, on the other hand, is divided, common sensation, and the sense of touch in the tip of the tongue, are annulled[577].

[575] Rapp *On the Fifth Pair*, p. 10. He found no branch of the fifth distributed to the tongue either in the swan or parrot, both of which have a very delicate taste; in these two instances the tongue is supplied from the par vagum and glosso-pharyngeal.

[576] See my Elements of Comparative Anatomy, § 325 and 326.

[577] Panizza made many experiments upon the division of different nerves in dogs, with every precaution requisite to arrive at accurate conclusions. After recovering from the depression into which he was thrown by the operation, a dog whose glosso-pharyngeal nerves had been divided, was found to lap water and to masticate with as much ease as if he had suffered no kind of injury. But he had now obviously no other guide in the choice of his food than the sense of smell, so that he ate up the most unsavoury and injurious articles if they had no smell, or if the odour was concealed by one that was grateful to him, with the same greediness as he would have done had they been of the most agreeable flavour. The animal ate pieces of plain meat, and of meat that was mixed with colocynth, with like apparent relish, and drank milk and water dosed with the same bitter drug, as if they had been quite pure. Not content with eating the meat which had been dipped in a solution of extract of colocynth, he also lapped up the liquor. The lingual nerves of another dog were divided at the same time as the glosso-pharyngeals of the last. This second animal, among several pieces of flesh which Panizza threw to him, bolted a bitter one very hastily; but scarcely had it reached the œsophagus, when it was rejected by vomiting, upon which the dog whose glosso-pharyngeals had been cut, seized the morsel and swallowed it comfortably. That this animal still possessed common sensation

These experiments, taken in connection with the obvious anatomical arrangements, enable us to draw an interesting parallel between the tongue as the organ of taste and the organs of the other higher senses. As in the tongue, so in the eye, the ear, and the nose, do we find a nerve of special sense, a nerve of common sensation, a muscular nerve, and in addition fibrils from the sympathetic combining in the performance of a common function[578].

The experiments that have been performed with sapid substances applied to different parts of the tongue have nevertheless given different results. In some persons the nature of each is immediately recognized when it is applied to the point of the tongue—at least bitter, sweet, and salt substances have been detected in this way. Others, again, seem to have no idea of the nature of sapid bodies

in the tongue, was made evident by the efforts he made to escape as often as the member was pricked with a needle. These experiments, so decisive in their results, were repeated and fully confirmed by Valentin (*Repertorium*, B. ii, S. 219). Very lately, too, Stannius has made many experiments, and declares for the views of Panizza in everything. On the other hand, Gurlt, Müller, and Kornfeld, are led by their experiments to conclude that the glosso-pharyngeal is not the nerve of taste, an animal which had had it effectually divided on both sides still preserving that sense. It is very necessary to be aware that we are liable to many errors in performing such experiments; dogs when they are hungry will devour meat however strongly seasoned with bitter drugs, when all the nerves are entire. Müller's *Archiv* f. 1837, S. 277, and Kornfeld, *De Funct. Nervor. Linguæ Experimenta,* Berol, 1836.

[[578] Had the very remarkable and interesting observations of Mr. Patrick Blair, a Surgeon of Dundee, not been lost sight of, we should scarcely have had the true anatomy and physiology of the nervous system to search for in the beginning of the nineteenth century; the proper course to be pursued seems clearly indicated by Mr. Blair more than 130 years ago. In his anatomical description of an elephant which died near Dundee, in the year 1706, he makes use of the following very remarkable language: "This extraordinary part [the proboscis] did not want for nerves sufficient for it, no more than for blood-vessels; for first it has the nervus olfactorius, whereby it is endued with a most acute sensation of smelling; 2*d*, The second branch of the fifth pair, by which it has so acute a sensation of touching or feeling; and 3*d*, The hard portion of the nervus auditorius, which seems to be chiefly destined for the different motions of the proboscis; for the muscles of the proboscis being divided into several fasciculi, each of them has a branch of this nerve dispersed in it. * * * Thus you see how signally this member is endued with instruments for the performance of its different functions: and it has a great analogy to the eye by its three pairs of nerves, viz: one for its seeing, analogous to [that in] the other for smelling, one for its pathetical motions, analogous to the acute sensations afforded to the other by the 5th pair, and one for the motions of its other muscles, analogous to [those conferred by] the hard portion to the other. *Philos. Trans.*, vol. xxviii, (1709.) p. 84, 85. R.W.]

applied exclusively to the tip of the tongue; they must be brought into contact with the root of the organ before they are known[579]. Mechanical and galvanic stimuli applied to the upper and under surface of the tongue engender indefinite sensations, which cannot properly be referred to the category of gustatory impressions[580]. At the root of the tongue every slight stimulus,—simple contact of a clean point, moistening with an insipid solution, etc. excites a sensation, which, in general, is spoken of as bitter[581]. In irritable

[579] Upon this point we have many opinions. In the course of the experiments which I performed on myself and several other persons some time ago, with four different substances, (vinegar, and solutions of quinine, sugar, and salammoniac, applied by means of a fine glass rod,) it was found that distinct sensations of taste were only excited when the papillæ circumvallatæ and posterior parts of the tongue were touched. The tongue being kept still we could not tell whether it was the sweet or sour, the bitter or saline solution that was applied to its tip—there was no sense of taste in this part. It is therefore very necessary to guard against being misled; the nose and eyes must be closed, and great care taken that no other part of the mouth, save that which is under consideration, be touched, particularly that the saliva does not distil backwards towards the root of the tongue. In my experiments I observed that the tactile power of different parts of the tongue was always inversely as the gustatory faculty: at the apex, for example, the sense of touch is at the maximum, (vide Annot. 565); in the middle it is only half as keen, or the points of the compasses must be elongated twice as far, in order that a two-fold impression may be induced; and towards the root the ratio is still farther increased. See Froriep's *Neue Notizen*, No. 75, 1837. Valentin employed sugar and alum in his experiments upon this point. (*De Funct. Nerv.* p. 116.) He concluded that the anterior half of the dorsum of the tongue in the majority of subjects, possessed no power of distinguishing savours; in one individual only did he find the thing otherwise. The inferior aspect of the tongue on the contrary had the faculty of tasting in the greater number of men, either through its entire extent, or in particular places. In the individual who could taste with the tip of his tongue, the faculty of tasting with the lower aspect of the organ was wanting. The base of the tongue in every case possessed the faculty of taste in the greatest perfection. Arnold, *Elements of Physiology*, (*Lehrb. der Physiologie*, B. ii, S. 547), agrees with those who regard the fifth as well as the glosso-pharyngeal as the nerve of taste, and maintain that the latter has only a finer perception of gustatory impressions.

[580] I agree with Rudolphi, that galvanism occasions no distinct impression of taste; that the tongue having a pair of zinc and copper plates applied to it, only perceives an indefinite metallic sensation; in other words, experiences the galvanic stimulus. The majority of persons have no perception of what it was formerly asserted they had, viz. an acid taste when the tongue is placed between a plate of zinc on its upper surface, and one of silver on its lower surface, and an alkaline taste when the disposition of the plates is reversed.

[581] I have made the experiment many times: on applying a drop of distilled water to the root of the tongue, or merely touching it with a clean dry glass rod,

subjects, a feeling of nausea is at the same time very apt to be aroused, accompanied with the closely allied reflex act of retching. On the whole, it would seem that the sense of taste was most acute towards the root of the tongue, where the greater number of the branches of the glosso-pharyngeal are distributed to the papillæ circumvallatæ. When we observe, as we shall presently, that many substances taste differently at the tip and at the root of the tongue, it would seem that there was some difference in the functions of the nerves principally distributed to one or the other of these parts.

§ 282. Substances which are truly sapid,—which do not merely excite an indefinite or tactile sensation in the tongue, must be soluble in the saliva, and impregnate the papillæ. Here being imbibed, they operate immediately upon the primitive fibres, which in the papillæ circumvallatæ form numerous convoluted rosettes or glomerules, similar to those of the tactile papillæ of the fingers. It is easy to follow large twigs of the glosso-pharyngeal nerve into these papillæ circumvallatæ[582].

When we would gain a complete knowledge of the sapid properties of any body, we have to call in the assistance of compound muscular movements, exactly as in the case of touch. The substance—and the liquid is the best form—is made to diffuse itself slowly over the entire surface of the tongue, which is pressed once and again to the roof of the mouth; finally, the act of deglutition is performed, an act which is quite indispensable to judgment

many persons have assured me that they experienced a slight bitter taste. A similar and decided sensation of bitterness, if the phrase may be used, with a distinct bitter after-taste, is experienced when the base of the tongue is depressed with the point of the dry finger; this feeling at the same time passes into that of nausea, and if the pressure be persisted in, retching follows.

[582] It may be said that the posterior third or rather more of the mucous membrane of the tongue receives branches of the glosso-pharyngeal; the remaining anterior two-thirds are supplied by the lingual branch of the fifth, minute twigs of which can readily be traced into the mucous membrane and papillæ, and observed forming little plexusus around the foramen cœcum linguæ. Several papillæ about the middle appear to receive branches from both the ninth and fifth; the two nerves do not seem any where to combine and form terminal plexuses. We have as yet no microscopical representations of these structures. Arnold has given very beautiful figures of the vascular plexuses of the tongue and its different papillæ. (*Tab. Anat.* x. Fig. 14—20.)

in matters of the palate, and to which we are, by nature, strongly impelled. Many substances have at first a very different taste from that which they have at last; we therefore speak of an *after-smack* in connection with many articles[583]. This after-taste is apparently owing in part to more extensive diffusion of the substance by means of imbibition, partly to greater excitement of the nerves through more prolonged and intimate contact, and partly to the probable difference in the sensations appertaining to the glosso-pharyngeal and the lingual branch of the fifth; in other words, to the difference of effect upon the tip and upon the root of the tongue[584]. What has now been said is to be understood as having reference to chemical soluble substances; what are called mechanical savours are nothing more than tactile impressions upon the tongue[585].

§ 283. Taste, like every other sense, is susceptible of being edu-

[583] According to Horn, there is a general and striking similarity in the after-taste in all circumstances,—it is usually bitter. The substances that contain tannin, however, prove a remarkable exception to the rule, the after-taste with these being almost invariably and persistently sweet.

[584] Horn has made many experiments upon this point, and given tabulated views of his conclusions in his work, distinguishing the effects according to the nature of the papillæ. To the papillæ circumvallatæ the greater number of substances tried, (more than three-fourths,) tasted bitter, or bitter with a mixture of some other taste. The bitter and alkaline or saline was much more common than the bitter and sour. The papillæ fungiformes could not be made out as possessing any peculiar gustatory sensations. To the papillæ filiformes the predominating impression was one of acidity, so that two-thirds of the substances essayed were pronounced sour; the bitter savour was, however, still perceived along with the greater number of vegetable substances, particularly when applied to these papillæ, the bitterness being very commonly associated with a perception of sweetness. The sweet, bitter, and other varieties of savour, are therefore neither connected with particular substances nor with particular species of papillæ. (*loc. cit.*, p. 96.)

[585] To this belongs, for instance, the rough, austere, or astringent taste—more properly sensation. Perhaps the discrimination of chemical substances,—of such penetrating articles as acids, in so far as they are already known, upon the tongue, by some persons, may be connected with the peculiar tactile sensation which they excite in the fifth pair, in the same way as we distinguish different stuffs—silken, woollen, cotton, &c., by handling them. Many impressions, now referred to the head of taste, would then come to be regarded as merely delicate tactile perceptions, by which repeated experience enables us at length to distinguish certain chemical qualities through the medium of simple mechanical qualities.

cated to a great degree of acuteness and delicacy[586]. The sapid properties of many substances are distinguished much more readily and accurately when certain other articles are tasted immediately before them; and whilst many articles taste agreeably in combination or succession, many others do not: sharp wine and bitter beer, for example, are not pleasant along with sweets, fruit, etc. There is, therefore, a harmony of tastes, as well as of colours and tones, although it is not so easy to determine the laws of the first as of the two last. When different substances having very decided flavours are tasted in quick succession, the gustatory impression is not merely modified or altered; all definite perception of taste is annulled. If, for instance, a variety of substances—bitter, sweet, sour, salt, etc., have been applied to the tongue in succession, by way of experiment, or if we go on tasting red and white wine alternately for a time, the sense of taste is temporarily so much blunted, that we are no longer in a condition to distinguish accurately between one savour and another.

In reference to tastes, moreover, there is far more of subjectiveness, than in reference to the higher senses, hearing, for example, in as much as it is much more of what may be called an instinctive sense than this. Our tastes alter with our years, a circumstance the physical cause of which, undoubtedly, resides in the nutritive function: many articles of diet that were grateful in our childhood are disgusting in later life; and, on the contrary, many things which, as children, we took with distaste, are relished when we come to be men[587].

With regard to the impressions of taste which we experience in sickness, independently of the food or drink we may have taken,—pathological subjective tastes, as of bitterness, sweetness, etc.,—these are all consequences of internal organic stimuli, or rather of alterations in the chemical or physical processes of the internal organism, particularly the stomach. The state of the mucous membrane of the stomach is generally allowed to be reflected in that of the tongue[588]. In a general way, such states, as well as all or the

[586] As examples, the delicate palates of the professed wine-tasters and tea-tasters may be quoted, these persons being able to distinguish the nicest shades in the flavour of the different kinds of wine and tea submitted to them, and to affix the relative value of each, with great accuracy.

[587] Vide what has been said of the changes that take place in the structure of the intestinal villi at different ages, § 138, and the appended Annotations.

[588] See the observations of Beaumont, § 136, and Annotations connected.

major part of the so styled organic irritations, may be referred to the secretion of a chemically altered saliva, to the presence of the elements of bile in the fur of the tongue, etc., so that in their causes they are not so different from objective tastes as at first sight appears. They do, in fact, fall under the category of effects of sapid agents in contact with the nerves of taste.

Of Smell.

§ 284. The sense of smell takes cognizance of the particles of odorous bodies which are held suspended or dissolved in the air. In the act of inspiration these particles are brought by the current that is streaming through either nostril into contact with its mucous membrane where they act upon the olfactory nerves. The sense of smell inheres in the mucous membrane that covers the cribriform plate of the ethmoidal bone, the whole of the superior, and a portion of the middle turbinated bones, upon all of which, branches of the first pair of nerves are plentifully distributed [589].

§ 285. There can be no doubt about the exclusive inherence of the sense of smelling in the olfactory or first pair of nerves. This fact is proved: 1*st*, By direct experiments upon animals. When the olfactory ganglia are divided in rabbits, the animals feel no pain, and none of their muscles are convulsed[590]. They readily recover from the operation, but they have lost all susceptibility to be affected even by the strongest odours, whilst the soft parts in which the olfactory nerve is distributed, still retain their impressibility to ordinary stimuli. This impressibility is acquired from the branches of the fifth pair, to which at one time, and that very recently, there was a disposition to ascribe some share in smelling. 2*d*, By the data afforded by comparative anatomy: in all animals endowed with a keen sense of smell, the first pair of nerves is very large, —much larger relatively than in man. 3*d*, By pathological facts: there are now many cases on record in which the olfactory nerves have been found either absent or variously altered organically in

[589] Among special treatises on the organ of smelling, that of Scarpa, *Disquisitiones de Auditu et Olfactu*, Ticin., 1792, of Söemmerring, *Icones Organi Humani Olfactus*, 1809, and of H. Cloquet, *Osphrésologie ou traité des Odeurs, &c.*, 1821, may be mentioned, as also Moeller's dissertation, *De Odorum Effectibus*, Berol. 1826.

[590] On this topic, consult the experiments of Valentin: *De Funct. Nerv.*, p. 10.

the bodies of persons, who during their lives had had no sense of smell. In other cases, again, in which persons have complained of unpleasant smells, from a subjective or inherent cause, changes of structure have been found at the roots of the olfactory nerves, or in the brain over them[591]. Every time we catch cold, indeed, we have assurance of the truth under discussion, inasmuch as the sense of smell is blunted or lost for the time, whilst the susceptibility to ordinary stimuli remains, or is even increased. Observations on living individuals, who without smell have nevertheless been abundantly sensible to ordinary stimuli, and exhibited the reflex motions that characterize excitement of the branches of the fifth pair, also vouch for the distinct office of the two nerves supplied to the nose[592].

§ 286. An organ of smell is met with in all vertebrate animals, at least there is always a particular nerve distributed upon a sac or cavity lined with mucous membrane, which corresponds in all respects with the olfactory or first pair, in its highest state of development. Even in those animals that breathe by means of

[591] The cases observed by Morgagni, Loder, Rosenmüller, and others, are alluded to; see the general review of them in Rudolphi's *Physiology*, ii. p. 116.

[592] Vide § 287. [Mr. Hunter criticised this complex distribution of nerves much more ably than many of his successors have done. In a paper, entitled, "*A Description of the Nerves which supply the Organ of Smelling*," he tells us that in his dissection of the nose, "he found several nerves, principally from the fifth pair, going to and lost upon the membrane of the nose; but I suppose," he continues, "that they have nothing to do with the sense of smelling; it being more than probable that what may be called organs of sense, have particular nerves, whose mode of action is different from that of nerves producing common sensation, and also different from one another." He proceeds: "Although the organs of sense [besides their special nerves] may likewise have nerves from different parts of the brain, yet it is most probable that such nerves are only for the common sensations of the part, and other purposes answered by nerves. Thus we find nerves from different origins, going to the parts composing the organ of sight, which are not at all concerned in the immediate act of vision; it is also probable that the parts composing the ear have [different] nerves, and if we carry this analogy to the nose, we shall find a nerve which we may call the peculiar nerve of that sense, and the other nerves of this part derived from other origins, only conveying common sensation, and only intended for the common acts of the part." (*Obs. on certain parts of the Animal Economy*, 4to, Lond., 1st ed., 1786, 2d, 1792.—Mr. Hunter, 70 years and more after Mr. Blair, again pointed out the proper path of investigation in regard to the functions of the nervous system; but the seed he scattered still fell upon a barren soil; men's minds were not prepared to receive and cherish it into new and productive life. Vide Annots. 525, &c. R. W.]

gills, and that have no nasal passages communicating with the pharynx, the olfactory nerve forms decided plexuses, and indeed is often much larger than it is in many of the mammalia that live in water[593]. In birds, among which the sense of smell is often very acute, we already observe a great analogy with the mammalia and man. In the roomy nostrils of these creatures we find three, generally cartilaginous, turbinated processes, of which the middle one is the largest, and presents itself as an involuted membrano-cartilaginous plate. The superior process is rather a kind of vesicular eversion of the cartilaginous walls of the nose. It would seem that the olfactory nerve is only ramified over the surface of this; and that the two inferior turbinated processes are supplied by branches from the fifth pair[594]. Among mammalia, great variety is apparent. In the cetaceans, (the porpoise,) the olfactory nerve is so slender that it has been overlooked by many anatomists. It is present, however, but in the form of an extremely fine thread on either side; and the cribriform plate of the ethmoid bone in relation with it is also rudimentary. It is among the keen nosed

[593] As we must conclude that odours are only perceived when they are dissolved in the atmosphere, the great development of the olfactory nerves in fishes appears the more remarkable, seeing that they are merely rudimentary in the cetaceous tribes. Perhaps in fishes they serve as the instruments of tactile impressions of a peculiar kind, are rather influenced by the chemical effects of the substances held in solution by the water, and stand in lieu of the sense of taste, which, if we may judge from the imperfect and often entirely absent tongue, must be very defective in the whole class. [The atmosphere, with reference to the higher mammalia and man, is but the vehicle of odorous particles, which only come to be perceived after they are dissolved in the mucus that bedews the nasal membrane; when this is dry, we have no sense of smell; water must therefore be at least as apt a vehicle for the conveyance of odorous particles as air; hence, and in harmony with this fact, the large development of the olfactory nerve and corresponding peripheral apparatus in fishes, which beyond all question have a very acute sense of smell; the whale tribes, again, whilst they breathe through their nostrils, do not seek their prey in the air, and no end would have been answered by the distribution of an ample nerve of smell over an extensive labyrinth of winding passages at the inlet to the respiratory system. Hence are they virtually without smell.

[594] This is also the case with mammalia, and it is the more remarkable, seeing that in the carnivora and the rodentia, the immense development of the inferior spongy bone appears to bear direct reference to the very delicate smell which they enjoy. This relationship may perhaps indicate that certain substances which exert their influence rather in a chemical or mechanical way, and which are, therefore, somewhat improperly designated odours, are perceived by the nerves distributed to the inferior spongy bone. There is here, very obviously, a combination of the same kind, as we perceive in the tongue.

mammals that the olfactory nerve attains its highest development; here, it is often infinitely larger, both absolutely and relatively, than in man. It is, in fact, a hollow, club-shaped, or lobular mass, plentifully intermingled with ganglionic corpuscles, and situated beneath and in front of the anterior lobes of the brain in the carnivora, ruminantia, pachydermata, rodentia, and marsupiata. There is at the same time, and in harmony with this large evolution of the nerve, a very ample cribriform plate, perforated with an infinite number of holes leading to an amply developed ethmoidal labyrinth. Among the turbinated or spongy bones, the inferior is that which is more especially developed. The central bony plate produces a multitude of offsets, so that the transverse section resembles a tree that spreads from a point into numerous branches. This implies, that the nasal fossæ are very ample, which they are in fact; but in addition, every precaution is taken to have the largest amount of surface within the smallest possible space[595]. The cavities supplemental to the proper nasal meatus are in general present, but exhibit the greatest diversities in their development in individual genera, and often in closely allied families. The frontal sinuses generally exist, and are occasionally, as in the elephant, of wonderful extent; the same may be said in regard to the maxillary sinuses; in the elephant they, too, are extensive, but in other animals possessed of a very acute smell, such as the carnivora and rodentia, they are altogether wanting, all of which gives us the assurance that these cavities stand in no particular physiological relationship to the proper organ of smell[596].

§ 287. A comparison of the anatomical structure of the organ of smell in man, with that of the animals most closely allied to him, demonstrates the fact which indeed had already been learned from experience, that whilst he surpasses many species in the faculty of smelling, he is in his turn surpassed in this particular, by a much greater number. When the olfactory nerve of man is compared with that of the dog, for instance, we see, that with a brain vastly

[595] This development of the inferior spongy bone is most remarkable in the dog; it is much less conspicuous in the cat.

[596] The views of those physiologists who maintain that the sinuses and adventitious cavities were a kind of store-chambers for odours, and are particularly developed in animals gifted with a fine scent, must be taken with abatement.

smaller, the olfactory nerve of the animal is nevertheless four or five times larger than that of the human subject. In man, the olfactory nerve is composed of a number of extremely delicate fasciculi, which penetrate the gray substance in the fissure of Sylvius, and may be traced in three principal divisions for a considerable way into the interior of the hemisphere of the brain. In the new-born infant, the olfactory nerves are not so long as they are later in life; they bear a strong resemblance to the olfactory lobules of mammalia, save that they are relatively much smaller. The primitive fibrils of the olfactory nerve are extremely fine, and readily become varicose, (§ 231). They traverse and form plexuses in the midst of the excessively delicate mass which constitutes the olfactory ganglion. This ganglion appears to be regularly hollow in the embryo, it is more rarely so in the child, and in adult age it is solid; in the majority of mammiferous animals it continues hollow through life[597]. Upon the cribriform plate of the ethmoidal bone, the primitive fibrils collecting into delicate sheathless bundles, and unaccompanied by any ganglionic corpuscles, quit the ganglion, pierce the bone, and having reached the mucous membrane of the nose, they begin immediately to form dense plexuses under the surface of the membrane which covers the ethmoidal cells, the superior spongy bone, and partly, also, the middle spongy bone. We are altogether uncertain as to the mode in which the olfactory nerve terminates[598].

[597] The olfactory nerve, as we have already seen, is evolved in the embryo, from the anterior cerebral cell, (Vide *Generation* and *Development*, Book i.) It long shows a cavity in its interior, as it does in the mammalia through life, which communicates with the lateral-ventricle, and like this, appears endued with a delicate ciliate epithelium. In the course of the third or fourth year, the base of the root, which up to this time has been of some breadth, begins to extend in length, and becomes more slender. The sinuses connected with the organ of smell also begin to be slowly developed after birth; and in harmony with these changes, the sense of smelling gradually improves; for it is certain that children, during the first years of their life, have a much less perfect sense of smell than they acquire afterwards.

[598] Valentin states very correctly, that the primitive fibrils of the olfactory nerve are only surpassed by those of the optic nerve, in delicacy. The same excellent authority inclines to believe that ganglionic globules, or structures extremely like them, may also be discovered on the inner aspects of the more delicate plexuses, a statement which I hold to be scarcely determinable one way or the other. We are yet without any method, so far as I know, of preparing the mucous membrane of the nasal cavities in such a way, as admits of our following

§ 288. Odorous substances, which do not at the same time affect the mucous membrane mechanically or chemically, and so irritate it, are brought by the act of inspiration into contact with the mucous membrane of the nose. The more strongly we inhale, the more intense is the impression upon the organ of sense; we at the same time close the mouth in order that the whole of the air inspired may enter by the nose, and we dilate the nostrils to give a freer passage to the current; and it is worth observing, that the alæ nasi are generally well developed in animals that have a sharp scent. When we smell at any object, when we would accurately appreciate its odorous properties, we farther make repeated short inspirations, and use efforts to secure the access of the odoriferous particles as high up in the nose as possible. The nose is beautifully adapted to this; for the air streaming through a narrower opening into a wider cavity, naturally becomes retarded in its course, and is brought more intimately into contact with the mucous membrane. The odorous particles dissolve in the moisture of the mucous membrane, which they penetrate by imbibition, and so attain the nerves. When the mucous membrane is dry, we either smell imperfectly, or not at all. Pure odours only affect the olfactory nerves,—to this category belong the greater number of the odours of flowers, and of many animal substances, musk among the number. Chlorine, ammonia, acetic acid, etc., appear to act as irritants upon the fifth pair, and are, therefore, felt and recognized by individuals who have little or no proper sense of smell[599], individuals in whom the olfactory nerves are either originally deficient, or have been destroyed. From the proximity of the brain, and the immediate connexion of the olfactory nerves with the cerebral hemispheres, the sensorium seems to be more readily affected by stimuli applied

the primitive fibrils of the olfactory nerve to their terminations. I have not myself been able to come to any conclusion on the subject. The principal ramifications of the olfactory nerve upon the mucous membrane, are figured by Söemmerring, (*De Org. Olfactus*) and by Arnold, (*Tab. Anat.*, T. ix.)

[599] See § 284. I am acquainted with a young man and his sister, who have no sense of smell whatsoever; the parents, however, and another sister, are endowed, in respect of smell, like other people. Ammonia applied to the nostrils of the young man in question, produces a distinct stinging odorous sensation. No one at the present day, with the exception of Magendie, (*Journ. de Physiol. Exper.* T. iv, and *Elemens de Physiologie*, T. i.), attributes any perception of smell to the nasal branch of the fifth nerve. Vide Valentin, *De Funct. Nerv.*, p. xi.

to these than to any of the other nerves of sense[600] It is well known that delicate persons, especially females, are apt to faint when exposed to strong perfumes[601]. Various reflex phenomena, too, vomiting, among the number, occur even in the strongest, under the influence of noisome stenches:—a sickening smell is a very legitimate expression.

§ 289. The organ of smell exhibits an unusual number of subjective phenomena, and of individual peculiarities. Some persons are remarkable for the great delicacy and keenness of their smell[602]. It is among animals, however, that this sense is met with in its highest perfection, among which it is indeed most intimately connected with the two instincts that are of the highest importance to the individual, and to the species,—the instinct by which food is taken, and that by which the kind is continued[603]. Experiments instituted on purpose, satisfy us that different individuals have very different powers in appreciating and judging of odours; the odours of flowers even impress different persons very differently[604]. The judgments upon what are to be held pleasant and what unpleasant smells—perfumes or stenches—are also extremely various. Anti-

[600] [The effect of strong and pungent odours in recalling sensibility, is probably less to be ascribed to their action on the first, than on the branch of the fifth distributed to the nose: no one thinks of applying otto of roses, or musk, to the nostrils of a lady who is threatened with fainting; ammonia and aromatic vinegar, which act as simple irritants, are the articles sought after. R. W.]

[601] It may often be doubtful whether certain odours exert their influence upon the sensorium, immediately through the olfactory nerves, or secondarily, by being taken up by the blood in the lungs.

[602] Small-pox, measles, fever, menstruating women, &c., are recognized through the sense of smell, by a few physicians, indeed, but by these with the greatest certainty. The American Indian, according to Humboldt, will distinguish a white from a black, and individuals of their own race from others, by the sense of smell.

[603] Hence, the delicacy, and at the same time diversity, of the scent in carnivorous and herbivorous animals; the smell of putrifying animal substances, which attracts the creatures that live on carrion from great distances; the odour of the female parts of generation, especially in the season of heat, in which large quantities of a peculiar odorous mucus are secreted, &c.

[604] Turner (see Arnold's *Physiology*, ii. p. 561) made a series of experiments upon this point. He found that the flower of iris persica was pronounced of pleasant odour by 41 out of 54 persons; by 4 to have little scent; by 8 to be without all odour, and by 1 to be ill-scented; of 30 persons, 23 held the anemone nemorosa agreeable in its perfume; and 7 did not think it smelled at all.

parts, its fluids, etc., taken in connection with the deep and carefully defended situation of the entire organ, all assure us, that to a knowledge of the world of sound, a peculiar delicacy, harmony, and security of organization were indispensable[625].

§ 299. The external ear and other associated apparatus are mere conductors of sound. They receive sonorous vibrations, and they concentrate and conduct them inwards. In man and animals the external ear corresponds precisely in structure and function with the instrument which we call an ear-trumpet. The various elevations and depressions of the external ear, adapt it peculiarly to catch the sonorous waves arriving from opposite quarters. Those that impinge upon the concha from before and from the side, are most readily caught and appreciated. The form of the external ear, and the mode in which it is applied to the head, in various individuals, are by no means matters of indifference. In cases where the concha is small, shallow, and lies flat upon the skull, the hearing is in general less acute than it is where the outer ear is large, deep, and projects somewhat from the side of the head[626]. When the external ear is wanting or imperfectly formed, as also when it has been lost, the sharpness of the hearing commonly suffers[627]. The importance of the external ear, however, has rather

[625] It is easy by very simple experiments to have a demonstration of the different conducting powers of different media: a watch held in the hand is heard infinitely better when it is made to touch the teeth, than when it is kept free on all sides, or is laid upon the tongue. A small tuning fork suspended on a string introduced upon the point of a finger within each meatus auditorious, sounds like a great bell when it is slightly struck, &c. The peripheral nerves of the head have also been supposed to have some share in propagating acoustic impressions to the internal ear. In a case of paralysis of the facial nerve of one side, Arnold believed that the beating of a watch was less distinctly heard, when applied to the affected, than to the healthy side. This fact has been otherwise explained by Müller, who ascribes it to a reflex action, passing from the facial and fifth through the brain to the auditory nerve.

[626] Mr. Buchanan, of Glasgow, made some experiments on this point, and found that the best angle at which the ear can be set upon the head in order to catch the greatest number of sonorous pulses, is about 40°. If the concha be narrow, and lies flat against the head, so that it forms an angle of no more than 15° with the head, the hearing is rarely if ever acute; if the concha, however, be broad and deep, although the angle of attachment be small, still the hearing may be very acute.

[627] See in Lincke, (l. c. p. 443,) the conclusions of Bartholin, Haller, and others, from which it appears that persons who have lost their ears are usually duller of hearing than others.

been over than underrated; and numerous instances have occurred in which its loss has had little or no effect upon the sense of hearing [628]. The motions of the concha have a distinct effect upon the hearing. Animals, such as horses, which have very moveable external ears, furnished with numerous and powerful muscles, make use of them as a deaf man does of his ear-trumpet, directing them to the quarters whence sonorous pulses come[629]. In the human subject, the muscles of the external ear are generally but slightly developed, and the ear is either immovable, or susceptible of but a very trifling degree of motion. Some individuals, however, and certain savage tribes, have the power of raising and directing the ear forwards, so that it makes a larger angle with the skull when they listen[630]. The external ear is not a reflector only; by reason of its elasticity it is thrown into vibration, and so becomes a direct conductor of sound; when the meatus auditorius is stopped, bodies brought into contact with the concha are heard better than they are at ever so short a distance.

§ 300. The auditory canal—the meatus auditorius receives the sonorous pulses immediately, and conducts them to the membrane of the tympanum. The sound is at the same time strengthened by reflection from the walls of the meatus, and the resonance of the mass of air which it incloses; the walls of the passage, moreover, are solid conductors of sound. It is very possible that the dimensions of the meatus auditorius externus may exert an influence on the delicacy of the hearing[631]; one cause indeed of the comparative imperfection of hearing in infants and very young children, has

[628] This from the experience of Itard, Wepfer, &c. Vide Lincke, p. 442.

[629] In the horse, as many as seventeen different muscles of the ear have been described. See the representation of them which has been given by Gurlt: *Anat. of Domestic Mammalia*, Tab. 42.

[630] Almost every one must have met with persons having such a faculty. Haller has collected a list of cases: *Elementa Physiol.*, vol. v. p. 190; and Sir A. Cooper knew a young man, having perforation of the tympanum on both sides, who could depress the ear at pleasure, a faculty which he used freely in listening: *Philos. Trans.*, 1800.

[631] It is in this way that some explain the instinctive opening of the mouth which is so characteristic of eager listening; the dropping of the jaw is held to widen the meatus auditorius somewhat in its anterior part. Larrey and others have maintained, that the loss of the dentes sapientiæ, and large grinders, occasions hardness of hearing, by changing the position of the articular surface of the lower jaw, giving it a direction backwards, and upwards.—Larrey, in *Journ. Complement.*, T. xiii.

been referred to the shortness of the external auditory passage[632]. The precise influence of the cerumen upon the sense of hearing, has not been accurately ascertained; it would, however, seem to do more than prevent the ingress of insects and foreign bodies into the ear, inasmuch as when the passage is dry from a deficiency of cerumen, the hearing is less clear and perfect than it ought to be—the walls of the passage appear to enter into stronger vibration than is proper, and this either confuses the sonorous pulses, or in some other way impedes their due transmission to the tympanum. Too large a secretion of cerumen, on the contrary, and any accumulation of this substance within the meatus auditorius, are frequent causes of confused hearing, or of absolute deafness[633].

§ 301. In the cavity of the tympanum we observe extremely complicated relationships coming into play. The chain of auditory bones appears to serve both as an apparatus of conduction, and as one of tension. The membrana tympani is first a defence for the delicate internal ear: when it has been perforated, although the hearing may not have suffered materially, yet air, water, etc. being now apt to penetrate into the cavity of the tympanum, occasion inconvenience or a greater degree of excitement[634]. The membrane of

[632] Autenrieth and Kerner, (Reil's *Archiv*, B. ix, S. 324,) see in the absence of the funnel-shaped external ear, and the imperfect conducting powers of the bones of the head in children, the cause of the pleasure they take in loud, and to adults, often distressing noises, &c.

[633] The views we have upon the uses of the cerumen appear to have no surer foundation than mere hypothesis. According to Buchanan, the cerumen serves to render the sonorous pulses more melodious and more readily appreciated. Lincke observed that when the secretion of cerumen was defective, the delicacy of the hearing suffered. The end answered by the cerumen and the fine hairs at the entrance of the meatus auditorius, is commonly said to be the prevention of dust, insects, &c., finding access to the ear. The structure of the ceruminous glands had been little investigated until I gave figures of them, and showed them very analogous in constitution to sudoriparous glands—they consist of a duct and a simple lengthened sac, rolled up on itself, vide Fig. CLXXXVII. Buchanan estimated their number at from one to two thousand, which is probably too many. According to Berzelius, the cerumen is a kind of emulsion, a combination of a soft fat and albumen, besides an extractive matter of a peculiar nature, presenting itself in the form of a yellow and extremely bitter substance, soluble in alcohol, and another extractive matter soluble in water, and having lactates of lime and potash as ingredients.

[634] In the cases of perforation of the tympanum which Lincke has collected from Cooper, Himly, and Michaelis, pain, deafness, and inflammation were produced by the access of sharp cold air, of the water in bathing, &c., to the cavity

the tympanum is, farther, an admirable conductor of sound; it is so placed that the sonorous pulses which penetrate the meatus externus, as well as those that arrive by the Eustachian tube, fall upon, and throw it into vibrations, which, in reference to weak pulses, appear to act as condensers or strengtheners, in reference to more powerful waves, probably as refractors or reflectors. The different degrees of tension of the membrane, its thickness, density, state of dryness or moistness, etc. have all a decided influence upon its aptness to participate in the vibrations or sonorous pulses that reach it. The membrana tympani always vibrates synchronously or harmoniously with the ground tone [635]. The integrity of the membrana tympani, however, seems in no way indispensable to hearing; the membrane may be perforated and partially destroyed without any very remarkable implication of the sense ensuing. In such cases, nevertheless, the general rule is that a certain degree of dulness of hearing is the consequence[636].

§ 302. Besides the functions of the membrana tympani now mentioned, there are others, which, however, are rather referable to its connection with the chain of auditory bones, and depend especially on the tensor tympani muscle. When this muscle contracts, the handle of the malleus, and of course the part of the membrana tympani which adheres to it, are drawn inwards, by which the membrane becomes more funnel-shaped, and is rendered more tense than it was before. The unbracing of the membrana tympani follows apparently from the relaxation of the muscle just mentioned. The existence of any muscle or set of muscles with the title laxatores tympani is extremely doubtful; the textures that have been so designated have been lately described as simple tendinous or ligamentous bands, connecting the malleus to surrounding parts; but there is this

of the tympanum. The subjects of these cases all found it necessary to protect their ears by plugs of cotton wool.

[635] See an account of the experiments on the vibrations of tightened membranes, instituted by Savart. *Ann. des Chimie et Physique*, Tom. 26. Thin plates of wood, ivory, glass, metal, nay, the membrane of the tympanum itself, when thrown into vibration by pówerful tones in their vicinity, cast off fine sand or lycopodium powder strewed upon their surface.

[636] Lincke informs us, that from the cases he had collected, the hearing in general did not appear to have suffered. But in no instance can the history be held as altogether satisfactory and complete. Entire destruction of the membrana tympani, implying the loss of its support by the malleus, is always attended with dulness or loss of hearing.

to be said in favour of the muscular nature of these bands, that cross streaked fibres similar to those of the animal life have been observed in them[637]. There can be no question of the membrane of the tympanum being braced in different degrees according to the different intensities of the sounds that impinge upon it. It was an error, however, to suppose, as was formerly done, that the membrane of the tympanum is relaxed under very powerful sounds, and tightly braced under very gentle tones[638]. Physical experiments have shown, on the contrary, that the extent of vibration in vibrating membranes is lessened by every degree of increased tension[639]. A medium degree of tension in the membrana tympani, such as that in which it is habitually found, seems to be best adapted to the appreciation of delicate tones, inasmuch as by the distinct vibrations that are set up in it under their influence, they are more readily transmitted to the labyrinth. The membrana tympani is, therefore, fairly enough to be compared to the iris, which contracts ever the more powerfully the stronger the light that impinges upon it; in the same way, the membrana tympani is drawn in more powerfully in proportion to the loudness of the sound, and this in order to prevent too powerful an impression being made upon the labyrinth. Both motions follow from a reflected nervous action,—the stimulus to the nerve of sense is reflected through the medulla oblongata upon the motory fibrils of the iris and tensor tympani, which then contract. For this

[637] That the membrana tympani includes muscular fibres in its middle layer, as maintained by Home, Meckel, Buchanan, &c., is a view that is now generally abandoned. The middle lamina appears to consist of tendinous or elastic fibres. The muscular nature of the two bands that used formerly to be regularly described as muscles: the M. mallei externus, s. laxator tympani major, and the M. laxator tympani minor, has been called in question by Treviranus, Lincke, and Jo. Müller. I have not myself been able to find any such muscles in examining the ear of subjects in whom the tensor tympani was particularly well developed. Krause has, however, very lately maintained that in the M. mallei externus, when it is well developed, cross streaked muscular fibres may be distinctly recognised, a fact which if confirmed would place its muscular nature beyond all question. Krause does not admit any laxator tympani muscle. See his *Human Anatomy*. (*Handb. d. Mensch. Anatomie*, 2, Aufl. i. p. 495).

[638] Bichat and others. Vide Lincke, l. c. p. 478.

[639] The experiments of Savart show that slackly stretched membranes, when thrown into motion by sounding bodies in their vicinity, cast off sand with greater force than when they are more tightly stretched. In experimenting with the membrana tympani immediately, he concluded that the hearing was repressed or rendered duller, in states of high tension of the part. These experiments of Savart were confirmed by Müller.

reason it is that a certain degree of dulness of hearing in reference to very delicate tones accompanies a highly tense state of the membrana tympani[640]. It is easy to obtain conviction of this fact by some simple experiments on ourselves. When we attempt to inspire with the mouth shut and the nose held, the air contained in the cavitas tympani is pumped through the Eustachian tube and rarified, so that the external atmosphere then presses the membrana tympani inwards, upon which the hearing immediately becomes duller. The air again finding access to the tympanum through the Eustachian tube, the equilibrium between the two columns is soon restored. Something of the same kind virtually ensues when the effort is expiratory, instead of inspiratory: the air being forced through the Eustachian tube into the cavity of the tympanum, is condensed there, the membrana tympani is pushed outwards, and in this way rendered more tense. In either case the equilibrium of the column of air on either side of the membrana tympani is not immediately restored, by reason apparently of the very narrow passage through the Eustachian tube; and this circumstance explains the inconvenience that is experienced when atmospheres of very different density are encountered in quick succession, as, for instance, when the diving bell is entered, or when lofty mountains are ascended rapidly[641]. As the iris is accommodated at every instant to the varying intensity of the light, so is the membrana tympani incessantly harmonized in its state of tension with the nature of the sonorous pulses that impinge upon it. There appears to be this difference, however, between the two; that whereas the movements of the iris are automatical, those of the tensor tympani are not altogether so; they can, at least, be voluntarily excited in many individuals. When we fix our attention strongly on the organ of hearing, and make an effort, we are aware of a slight

[640] According to Wollaston and Müller, dullness of hearing is very rarely indeed general, or equal in regard to all sounds. Tones in a high pitch, even when weak, are commonly much better heard by deaf people than deep tones, however loud. In such cases the over-tension of the membrana tympani, in consequence of a kind of habitual spasmodic state of its tensor muscle, may be the cause of the deafness.

[641] Du Hamel and Colladon have given an account of the sensations induced by the compressed air of the diving bell. The former experienced very severe pain in the ears, the latter had only a feeling of pressure on the head. He heard the conversation of the work-people under the bell either with great difficulty or not at all. Froriep's *Notizen*, B. i. S. 97.

rustling or crackling noise, somewhat analogous to that which we perceive when we make a strong inspiratory movement whilst holding the nose and shutting the mouth[642]. In a general way, however, the action of the tensor tympani is only appreciated when, at the same time that the inspiratory effort is made, the soft palate is raised, and the act of deglutition is performed. It is possible, therefore, that the tension of the tympanum depends less directly upon the influence of the will, than upon the motion of the muscles of deglutition, by the contraction of which some air may be pumped out of the cavitas tympani.

§ 303. The Eustachian tube is beyond all question of essential consequence as part of the auditory apparatus. If it gets obstructed, there is forthwith singing in the ears, indistinctness of hearing, or positive deafness [643]. Its principal or sole office is to establish static equilibrium between the air included in the tympanum, and that of the external atmosphere (§ 303)[644]. The ciliary movements that go on over its mucous membrane may tend to the renovation of the air within the tympanum; but must be much more efficient in brushing out mucus, epithelial cells, etc., from its cavity. All else that has been said in regard to the uses of the Eustachian tube is either purely hypothetical, or obviously erroneous[645].

[642] Fabricius ab Aquapendente informs us that he could cause a noise in his ears at pleasure; and Müller (*Physiology*), and Theile (Schmidt's *Encyclop.* B. iii), have spoken of the point in detail. For my own part, I have never been able to induce these sounds save by raising the soft palate, and performing the act of deglutition.

[643] Every slight cold we catch that extends to the throat and Eustachian tube, satisfies us of the above. Cooper met with a case in which a preternatural contraction of the Eustachian tube interfered greatly with the free access of the air to the tympanum. The patient when he wished to hear was in the habit of first blowing with his mouth and nose closed till he had distended the drum; he then by means of gentle pressure with the point of a finger fitted into the meatus externus, forced out so much of the air again as was required to give the membrana tympani freedom to vibrate, and in this way he immediately exalted his powers of hearing. In the body of a day labourer, who for several years had complained of incessant noises in his left ear, Fleischmann found a barley-awn fixed in the left Eustachian tube, and projecting about a line beyond its extremity. (Hufeland's *Journal*, 1835).

[644] Hence the frequent use of probing the Eustachian tube, the object of which is the same as that which has been proposed to be effected less eligibly by perforating the membrana tympani, and trepanning the mastoid process.

[645] I allude among others to the idea of Henle, who compares the Eustachian tube to the hole in a violin, and the membrana tympani to the sounding board

§ 304. The tympanum—cavitas tympani—is a cavity indispensable to the free vibration of the membrane which bounds it externally, and is found in all animals that live in air. Moreover, the air which it includes reverberates, and the walls and neighbouring spaces and cells reflect sonorous pulses, which thus fall strengthened upon the walls of the labyrinth, and particularly upon the fenestra ovalis of the cochlea. The chain of bones, again, as solid parts, transmit the pulses from the membrane, even better than the air. The sonorous pulses received by the membrane, and reflected from the walls of the tympanum, centre in the ossicula, and undergo condensation, as it were, in them. The manubrium of the malleus receives the pulses from the membrana tympani immediately; from hence, they proceed to the head of the malleus, and then they go on to the incus and stapes, which carry them forward to the labyrinth. The step-like combination of the ossicula auditus proves no impediment to the transmission of sonorous waves; for by the laws of acoustics, waves are propagated in the line of their original direction, athwart cross-lying and slanting bodies[646]. There can be no doubt but that the auditory ossicles serve for the conveyance of sound; the idea that they serve exclusively as conducting media, however, appears to be extremely improbable[647]. A principal office of the curiously articulated chain of the ear-bones with their muscular apparatus, is unquestionably to exert a tensive influence on the labyrinth[648]. This view is vouched for, 1*st*, By the articulated form of the chain, and the necessity of the sonorous pulse proceeding through dissimilar media—from bone to

of the same instrument. The tone of a violin becomes damped when the holes are closed, in consequence of the air which it contains being now prevented from vibrating freely in harmony with the outer air and the walls of the instrument. The notions of Arnemann, Sprengel, Prochaska, and others, who held that the Eustachian tube existed for the purpose of conducting the proper voice of the speaker into the tympanum, and so making it appreciable to himself, are obviously erroneous.

[646] Savart showed that the conduction of sounds by plates which are connected together perpendicularly, and at different angles, took place in the direction of the original impulse.

[647] [648] Almost all recent physiological writers err in regarding the ear-bones as exclusively or all but exclusively conductory means; Carus has escaped the general mistake, and says with great propriety, that "the ossicula are by no means destined for the conduction of the sonorous waves alone, but that they partly also, and very essentially, constitute an apparatus of tension for the auditory sac."

cartilage, from cartilage to bone again, etc. Were simple conduction the principal consideration, a single unarticulated rod of bony substance would have been a much more efficient instrument than a chain of bones interrupted by articulations. 2*d*, The mobility of this chain, (particularly of the stapes, which has a peculiar and considerable muscle—the M. stapedius) and its entire anatomical structure is such, that not only do sonorous pulses pass through it to the aqua labyrinthi, but an actual pressure upon the membranous labyrinth, and a tension of the membraniform expansion of the auditory nerve are effected by its means[649]. The minuteness of the parts, and their inaccessability, unfortunately oppose a barrier to everything like direct experiment upon them. But we can see that the sonorous waves reach the labyrinth from the membrana tympani, in three distinct ways: (*a*) A portion of the pulses reflected from the walls of the tympanum reaches the external wall of the vestibule immediately, this being at the same time the internal or posterior wall of the tympanum; (*b*) Other pulses are thrown upon the fenestra rotunda, and in this way, and very directly, reach the cochlea; (*c*) A third set of pulses travel

[649] The stapedius, the smallest muscle of the human body, appears to stand to the labyrinth in the same relation as the tensor to the membrana tympani. It is very securely lodged in the funnel-shaped cavity of the eminentia papillaris, from whose opening the delicate tendon passes into the cavity of the tympanum, and becomes attached to the posterior edge of the neck of the stapes. When it contracts, the head of the stapes is drawn backwards, so that the bone librating, the posterior extremity of its base is pressed more deeply into the fenestra ovalis, by which the vestibular sacculus of the utriculus communis s. auditorius is rendered tense, whilst the anterior extremity of the base tends to rise out of the opening. (Vide Krause's *Anat.*, p. 498.) Müller thought that the action of the stapedius was unknown. The only effect hitherto ascribed to it, was the tension of the membrane, which connects the foot or base of the stirrup-bone with the fenestra. Arnold rightly refers to an effect upon the fenestra rotunda: the aqua labyrinthi must suffer compression, he says, by which the fluid in the scala vestibuli of the cochlea will necessarily influence that which is contained in the scala-tympani, so that the tension of the tympanum secundarium, or membrane of the fenestra rotunda, will be varied, and the faintest pulses of the air of the tympanum made apt to reach the fluid of Cotunnius. Arnold thinks it probable that the stapedius muscle, which receives a twig from the facialis or portio dura, comes into action especially during attentive listening, and that the delicacy of the hearing is increased in the manner indicated. As the long process of the incus is drawn inwards by the elevation of the stapes, it must be conceded that there is at the same time a movement in the entire chain of the ear-bones, the membrana tympani being likewise drawn inwards, and so rendered more tense. Vide § 202. The entire physiology of the muscles of

through the solid chain of ossicula immediately from the membrana tympani to the aqua labyrinthi. This last conduction must be held, upon acoustic grounds, the most powerful of any[650]. The presence and integrity of the stapes are of the very highest consequence to audition; if it be injured, or be wanting, perfect deafness is the consequence[651].

§ 305. We have nothing but hypothesis as to the manner in which sounds are transferred to the labyrinth and auditory nerve; yet by attentively considering the morphology and histology of the several parts, having at the same time an eye upon their evolution in the animal series, it would seem that something like firm footing may be attained in considering the subject. Several conditions for instance occur universally, and may therefore be looked upon as essential. Among these we have: 1*st*, The Aqua labyrinthi. Whatever the medium through which the sonorous pulses pass, be it air or water, are they transmitted immediately by the bones of the cranium, or through a chain of particular bones, or independently of these, in every instance are these pulses finally transferred to the auditory nerve by the medium of a labyrinthine fluid. The excitement of the several primitive fibrils of the auditory nerve might be expected to follow in the most equable manner possible under the influence of the pulsatory undulations of a fluid, which bathes them immediately, and penetrates between the meshes of their terminal plexus. In animals which live in air, the communication of the sonorous waves must also be more perfect through the medium of the aqua labyrinthi than it could have been without it, inasmuch as these waves are more readily transmitted from the air to fluids by means of an outstretched membrane, than by unyielding or immovable parts. 2*d*, An auditory sac surrounded

the internal ear requires a new and critical revision; in the course of which, comparative anatomy would be found of essential service.

[650] It is an ascertained fact that a small solid body set by means of a membranous rim within an aperture, conducts sonorous pulses from air to water—from the tympanum to the aqua labyrinthi—much better than parts connected solidly. The conduction becomes greatly more perfect still, when the solid body which closes the aperture is connected with the middle of an outstretched membrane in contact with the air on either side;—and this is precisely the arrangement that obtains in the tympanum. Vide Müller, *Physiol.* sub. cap.

[651] When the stapes is lost, the aqua labyrinthi escapes, and the expanded portion of the auditory nerve of course suffers. Lincke, p. 466.

by and filled with a fluid—the Saccus auditorius—which in its simplest form represents the vestibular sac, and hangs free, being only connected by the auditory nerve, and extremely delicate vessels, within a very firm cartilaginous or bony capsule, conditions which are found recurring even in the most complicated fashions of the labyrinth. By these means the greatest degree of protection and quiet are secured to the properly sensitive portion of the auditory nerve, at the same time that the most perfect and facile access to sonorous pulses arriving from every side is assured, and their reflection and condensation by the singularly solid substance of the capsule—the petrous portion of the temporal bone—is provided for. 3*d*, Solid bodies—otolithes—either hard stony masses, as in the cephalopods and bony fishes, or softer aggregations of minute crystals, inclosed in the interior of the auditory sac. It is difficult to decide as to how these otolithes comport themselves in reference to the sonorous pulses that reach the labyrinth, and many hypotheses have been broached on the point. Their general occurrence speaks loudly for a high degree of functional importance, and late direct observations upon their remarkable motions in invertebrate animals, seem to indicate that they are really in some way essential to the perception of sonorous pulses by the primitive fibrils of the auditory nerve[652].

[652] Too little weight seems hitherto to have been attached to these otolithes. Müller is of opinion that they would strengthen sounds by reverberation, even did they not come into contact with the membranes upon which the nerves are distributed; but as they actually touch the membranous parts of the labyrinth, these and the nerves connected with them receive impulses which, as coming from solid bodies, are even more intense than those that proceed from the water. Müller holds that the view according to which the small crystalline otolithes are thrown off from the walls of their including cavities during hearing, in the same way as dust is scattered from the surface of vibrating plates and membranes, is untenable on physical grounds, inasmuch as we do not perceive the smallest motion among the particles of dust suspended in water, under the influence of the loudest sounds (?). Breschet believes that the crystalline otolithes make an immediate impression upon the nerves, in consequence of which, the nervous tufts may possibly be more rapidly and more forcibly excited by sonorous waves. *Sur l'organe de l'Ouie, &c.*, p. 123. Cagniard Latour found by experiment, that molecular oscillations—during which the waves of the fluid seemed also to divide into globules—were more readily produced when rounded pebbles were placed in water; and he conceives that the concretions of the labyrinth may facilitate such molecular motions. *L'Institut*, 1833, No. 17. Lincke asks if it be not possible that the crystals of the labyrinth are shaken into figures in harmony with the several tones? The discovery by Siebold of the motions that take place

§ 306. The labyrinth is in all respects the most important part of the auditory apparatus. Whenever any defect in the structure, or morbid alteration of its parts, has been detected by dissection, there total deafness has been observed[653]. The end of the separation of the organ of hearing in man and the higher animals into vestibule, semicircular canals, and cochlea, cannot at this time be spoken of with any kind of certainty. Here we are in the region of pure hypothesis. We can nevertheless perceive in the arrangement that exists a means for securing an extension of surface, for bringing a larger number of the primary nervous fibrils into communication with the sonorous pulses, and also for reflecting and multiplying these. This, however, can hardly be the only object; the same end might have been variously attained, whilst in the structural relations of

in the otolithes of the snail, already referred to (§ 292), become particularly interesting, in connection with this hypothetical idea. The fact alluded to is described in the following words, by the able observer just named: "The otolithes inclosed in the auditory capsules of this animal, (the snail,) vibrate in so lively a manner, that one is almost tempted to imagine that they must be thrown together by the action of a powerful ciliary epithelium clothing the inner walls of the capsules; I have not, however, at any time observed a trace of ciliary apparatus within the capsules. The otolithes in the auditory capsules of the snail seek all to congregate in the centre of the cavities; the crystals that gain this position form a dense heap, and cling close together, much in the manner of iron filings under the influence of a magnet; the other crystals or otolithes that lie around the central group are in ceaseless motion; they appear as if they sought to penetrate the heap, but are often violently pushed off by this; still they return again, to be again thrust back, and so the dance is kept up. The inner capsular walls seem scarcely ever to be touched by these oscillating particles; when they are so, the particles are instantly repelled by them, and seem to become more restless than before. The motion greatly resembles that which we see when we place a little fineish sand with a drop of water upon one leg of a common tuning fork, and set the instrument into vibration."—No such direct observation as this is possible in any vertebrate animal. In man, according to Krause, the otolithes consist of parcels of whitish-yellow semitransparent bodies, of a crystalline aspect, which in part adhere firmly to the membrane of the labyrinthine sac, and which in part are suspended in the endolymph; in the ampullæ some few of these crystals of the smallest size are encountered; so also do they occur around the spiral plate of the cochlea, and in the fluid of the cochlear canal; here they are in some cases solitary, in others in parcels. *Handb. d. Anat.*, 2 Aufl. i. 502, 507.

[653] In the greater number of cases quoted, the semicircular canals were found abnormal in their course, structure, &c. The intimate connection of these canals with the rest of the labyrinth gives us assurance that this also was altered; but unfortunately the dissections which have hitherto been made of the morbid ear are seldom so complete and accurate as to afford grounds for physiological reference.

the internal ear there may be said to be identity in the entire series of vertebrate animals. With regard to the semicircular canals, in particular, that view is probably the most tenable according to which they collect the sonorous pulses from many points in the circumference of the petrous bone, and transmit them reinforced or condensed to the ampullæ[654]. This idea seems to be confirmed by the morphological arrangement of the canals, which is such that they comprise three dimensions of the solid mass which incloses them. The structure of the cochlea implies that the communication of sonorous pulses is here provided for in a variety of ways. The nervous expansion of the spiral lamina does not receive pulses from the aqua labyrinthi only, it receives them immediately also from the substance of the bone—from the firm walls of the labyrinth and the bones of the head [655]. The saccus vestibuli, in fine, through the chain of auditory bones, is the recipient of the most intense sonorous pulses; the waves which the ear presents to the sensorium as sounds impinge here most directly; and as the greater nervous expansion is also encountered here, and the largest number of crystalline particles is likewise here piled together, so would it seem that the impulse must best proceed from this point to the sensorium. That the several parts of the labyrinth are destined, one to judge of the direction whence sounds come, (the semicircular canals); another to take cognizance of articulate tones (the cochlea) etc., is a view that is sometimes demonstrably false, and sometimes improbable[656].

§ 307. The mode in which the primitive fibrils of the auditory nerve comport themselves in the perception of sounds, is altogether unknown. We can only see that the expansion of the auditory nerve is such, and so arranged, that every individual fibril must be powerfully impinged upon by the pulses of the surrounding lymph, and perhaps also by the crystalline deposit which here abounds. The terminal expansion of none of the nerves of sense affords such a

[654] This notion of the use of the semicircular canals is mainly derived from Scarpa; it was developed by Autenrieth and Kern. V. Lincke, p. 522.

[655] E. H. Weber gave much attention to the function of the cochlea: *Adnot. Anat. de Utilitate Cochleæ Prolus.* iv. v. vi., of which there is an abstract and commentary by Lincke. Weber is of opinion, that the sonorous pulses transmitted by the bones of the head are principally cognized by the nerves of the cochlea; those on the other hand that arrive by the membrana tympani, are perceived by the nerves of the membranous labyrinth, &c.

[656] For a more detailed account of these different views, vide Lincke, § 334—338.

favourable subject for observation as that of the acoustic nerve[657]. We see here with the greatest distinctness how the primitive fibrils, which are not by any means of excessive delicacy, form terminal plexuses upon the vestibular sac and ampullæ of the semicircular canals, in which the fibrils pass interchangingly from one fasciculus to another, and finally form distinct terminal loops (Fig. CCXXIV.) Similar terminal loops also present themselves upon the lamina spiralis of the cochlea. The number of primary fibrils of the acoustic nerve may be pretty accurately computed: they seem to amount to from 1000 to 1200[658]. The fibrils are so disposed that they seem to be struck or encountered by the pulses of the aqua labyrinthi, much in the same manner as the strings of a piano-forte are struck and thrown into vibration by the blow of the hammer. Now as each individual primitive fibril must receive its own separate impression, and farther, as each primitive fibril proceeds distinct to the brain, and so far as it is concerned transmits the received impression isolatedly, (§ 237,) it is easy to form an idea of the aggregate force of the multiplied impressions thus transmitted, and to see the ear adequate to appreciate all the variety of tones, high and low, loud and weak, harmonious and discordant, that constitute the world of sound. Several observers have held, that besides the primitive fibrils, there were also ganglionic corpuscles present in the terminal expansion of the auditory nerve; but the difficulty of tracing such delicate structures, and of distinguishing them from epithelial cells, leaves this point still questionable[659].

657 Fishes are the best of all subjects for observation here. The same structure exactly occurs in the higher vertebrata.

658 By direct reckoning I find about 100 primitive fibrils to each ampulla, which gives about 300 to each semicircular canal; we may allow at least the same number of fibrils to the two somewhat larger branches of the vestibular sac, and the cochlea may be held equal to these two taken together—this makes 1200 in all. The primitive fibrils of the auditory nerves I find about $\frac{1}{400}$th of a line in diameter; Krause estimates them at from $\frac{1}{840}$th to $\frac{1}{630}$th. Arnold's representations of the expansion of the auditory nerve upon the ampullæ and cochlea, can only be regarded as plans. The finer terminal loops form no such uniform nooses as he represents; but rather immediately before turning round, fall into very tangled plexuses. Fig. CCXXIV. is a faithful transcript of nature. Human subjects can seldom or never be had in so recent a state as to enable us to make out such delicate structures satisfactorily.

659 Valentin speaks of ganglionic corpuscles as occurring in the intumescentia gangliformis, at the point of division of the principal branches. See his

§ 308. Every concussion, every excitement or stimulation of the acoustic nerve, is appreciated by it as sound. Hence it is that it is not the pulses alone that sonorous bodies give out, and which form objective sounds, that excite sensations of noise. Here, as in all the other organs of sense, there are subjective impressions, or perceptions which may be elicited by stimuli that have nothing in common with sonorous pulsations. In consequence of the deep and well defended position of the internal ear, it is not so easy, as may be imagined, to produce these subjective impressions in the way of experiment, as it is in the case of the eye. We are therefore less familiar with the relations of the auditory nerve to stimuli other than sonorous vibrations. Such agencies as light, and heat, and chemical stimuli, cannot be brought into contact with the auditory nerve. The galvanic fluid passed into or through the ear, according to some, occasions a sound; but if it be easy to make a corresponding experiment upon the eye, and to satisfy ourselves of the subjective development of sensations of light by the action of the galvanic fluid there, it is just as difficult to excite a subjective impression of sound by its means[660]. The noises in the ear which we produce during experiments upon ourselves, are by no means subjective noises; they are succussions which are often appreciable to others by their sense of hearing. The pathological phenomena, such as singing, ringing, etc., in the ears, which occur along with congestions more general or more partial, with foreign bodies in the external meatus, etc., are evidently very ordinarily the effects of concussion or vibra-

Söemmerring, p. 466. Krause describes a layer of ganglionic corpuscles over the whole lamina spiralis, and upon the sacculi and ampullæ of the semicircular canals. *Op. Cit.* p. 507. Pappenheim, l. c. p. 62, speaks of ganglionic corpuscles in connexion with the branches of the auditory nerve; but he does not appear to regard the nucleated cells which he describes along with the peripheral expansion of the nerve as ganglionic corpuscles.—I do not, however, altogether follow him in his description. I have not from personal observation been able to satisfy myself of the existence of ganglionic cells here any more than in the retina.

[660] Ritter is frequently quoted as an authority on the production of sounds in the ear, by the galvanic current. I have made experiments on myself and many of my auditors, with no great force of galvanic current indeed, but always without any results. A powerful inductive apparatus being brought in the most varied ways into contact with the ear, the external passage being filled with good conducting fluids, flashes of light were always perceived in both eyes, never tones in the ears. Of 70 persons there were only 2 who thought they perceived sounds, but of the nature of these they could give no very good account.

tions identical with or productive of true sounds. The same must of course be said of blows upon the head, which are conducted as mechanical vibrations to the auditory nerve, in which such pulses necessarily excite corresponding impressions of tones. It were more legitimate to regard as subjective sounds those persistent impressions which, as in the eye, often remain like phantoms, after excessive stimulation,—for example, the singing in the ears after driving in a rough carriage along an indifferent road. To the same category may be referred the echo of a phrase of music or particular tune which is often so troublesome, the sudden and loud ringing in the ear which often comes on when we are sitting quiet, the rushing and hissing or ringing which occur along with great nervous weakness, and in the course of mental diseases when they so frequently occasion grave and very remarkable mistakes; farther, the sudden, generally dull sounds which we occasionally hear as we are falling asleep. It is very possible, however, that several of these phenomena may be occasioned by actual vibrations induced in the external parts of the ear, and conducted to the auditory nerve[661].

§ 309. It is only sound engendered in the external world that is capable of eliciting in the ear those varied phenomena which we distinguish as tones. The cause of the inherent diversities of tone, depends on the nature and number of the pulses or vibrations of the sounding body. A certain number of pulses or vibrations in a given time is indispensable to constitute a tone; the fewer the pulses, the deeper the tone. The most recent experiments show us that four vibrations or two pulses per second of the wheel invented by Savart, are adequate to engender a really appreciable tone. Thirty-two simple vibrations in a second, give the note C in the thirty-two feet organ pipe. The column of air contained in this pipe makes sixteen beats or pulses in one direction, which are equivalent to thirty-two double beats or vibrations in a second of time; twice as many beats or vibrations always give the octave of a note. The

[661] From the difficulty of ascertaining clearly what passes in the tympanum, t almost always remains doubtful whether the impressions generally styled subective, are not due to spasmodic contractions of the stapedius, elicited in states of special nervous susceptibility as reflex movements, and occasioning sonorous pulses in the aqua labyrinthi. The murmurs heard by Henle in his own person, when he passed the finger gently over the cheek, may probably be fairly explained in the same way.

note generally assumed as the highest in music, is the C upon the sixth ledger line, to engender which 16,000 vibrations per second are requisite; but the ear still distinctly appreciates notes much more acute than this, notes to the production of which, calculation shows that 48,000 vibrations per second are necessary.

By the word noise, we generally understand a succession of equal or unequal pulses in unequal times. Out of noises, however, true definable tones may be produced, by the noises in their more rapid succession approximating and forming regular sonorous pulses. Tones and noises not unfrequently become mingled by the fusion of regular and irregular vibrations. The strength of any sound depends partly on the nature of the sounding body, the rate of its vibrations, the synchronous vibration of other bodies, and its distance from the ear; partly on the degree of excitement of the auditory nerve. For this last reason especially, as well as from other circumstances already indicated, the strength of the same sound is variously estimated by different individuals. The *quality* of a tone depends on the quality of the sounding body. From the quality of the tone or tones we judge of the nature of the instrument which produces them[662].

§ 310. As in the case of all the senses, so in reference to the ear, do we observe many individual differences and peculiarities; in none of the senses indeed are these so numerous or so striking as here; the impression made by sonorous vibrations are almost as different as the individuals who perceive them. The acuteness of the hearing stands in no kind of necessary connexion with the power to discriminate tones from one another. Many persons having the quickest sense of hearing are entirely without what is called the musical ear. Still a certain succession of simple tones is felt as agreeable by the majority of individuals. But whilst one is powerfully affected by them, another is indifferent; and whilst the mass of civilized men distinguish concord and harmony from dissonance and discord, and declare certain series and combinations of tones as grateful to their ears, some few in every community, and savage tribes in general, have no perception of anything of the kind, and

[662] The subjects of this paragraph are all within the domain of natural philosophy, the elementary treatises of which may be turned to for farther information. One of the most convenient instruments for illustrating the production of acuter and graver tones is the *Sirene* of M. Cagniard Latour.

frequently prefer loud, harsh, and disagreeable sounds to the most melting melodies and dulcet harmonics[663]. In some individuals we meet with what may be regarded as true idiosyncrasies in reference to particular tones, which occasionally cause even painful feelings; we observe something of the same kind among animals[664]. Many circumstances connected with the perception of sound, stand in relation not to the outward reception of tones, but to the judgment upon them. Every sound, for example, is taken in by the two ears at once, whereby the intensity of the impression is increased. Nevertheless, the perception or consciousness, as in the case of sight, is single: we have a double impression, one on each tympanum, one on each retina, nevertheless we perceive but one sound, we see but one object. It seems doubtful whether double hearing ever occurs like double vision, as a pathological phenomenon[665].

Our capacity to judge of the direction and distance of sounds is an effect of our judgment. We in fact contrast sounds the nature of which is already known to us under the point of view of their strength, and so conclude as to their nearness or remoteness. We are therefore liable to many mistakes in estimating the distance of

[663] I think it unnecessary to enter at greater length on the consideration of musical tones in this place. The capacity to distinguish delicate shades of sound, such as constitute the tones and semitones of the musical scale, is innate, and is only strengthened and perfected by exercise; it cannot be acquired. Some persons who can perfectly well distinguish all the tones in the octave, cannot perceive any difference between one semitone and another of the diatonic scale of modern music. Other persons again who discriminate readily between high and low tones, cannot perceive the difference between a common chord struck properly and improperly—they are unaffected by harmony and discord. The tones of animals, such, for example, as the song of birds, is seldom reduceable to our system of musical notation, and yet the natural song of birds is pleasant to our ears.

[664] There are certain noises, such as that produced by scratching upon a slate, sharpening a saw, &c., which are felt as extremely painful by the generality of persons; and it is remarkable that such noises are not unfrequently productive of reflex motions in the skin—(goose-flesh). J. P. Frank mentions a man affected with tape-worm who could not bear the sound of the organ; Forestus, a beggar who was thrown into an epileptic fit by the sound of a child's drum; Boyle, a woman who lost her senses when bells were rung; [and Shakspeare tells us that certain persons "so often as they hear the drone of a Lincolnshire bag-pipe sing in their nose, cannot hold their water."] Dogs are well known to have a great antipathy to the sound of the violin, which often sets them howling piteously.

[665] But very few cases are positively known; they are related by Sauvages and Itard. In that of Itard, different high tones were heard by each ear.

sound; and our judgment on the point is so much the more insecure, as reflections, condensations, and reverberations are mixed up with the original sound. The same thing may be said in regard to the direction of sound, which we commonly judge of by the strength of the impression on one or the other ear, by the impression made being stronger in one position of the ear than another. Practice enables us here, as in all circumstances in which the intellect is brought into play, greatly to improve our faculty of estimating the strength and direction of sounds. The co-operation of the mind is therefore needful in connection with the operations of the ear, as well as of every other organ of sense, although there is perhaps none from the monitions of which the mind is so apt to free itself: when we are absorbed in reflexion, for instance, we do not hear—we are not aware of many sounds that take place around us, but which certainly make their way to the internal ear with the same force and precision as they do when our attention is directed to them. When, on the contrary, we would hear distinctly—when we listen, we put our whole soul, as it were, into our ears, and at the same time, consciously or unconsciously, we bring the entire apparatus that conducts to the labyrinth into the most favourable position for catching and conveying sonorous impulses.

CHAPTER III.

OF VISION.

Preliminary Observations.

§ 311. The eye is an optical instrument of singular perfection. To describe and to understand the functions of its several parts, implies a knowledge of the laws of light and of the science of optics, which are of course treated of fully in elementary works on natural philosophy. Light, however, like sound, exists to us only in virtue of our possessing a nerve endowed with a special energy in relation with this element, principle or power—the optic nerve, the peripheral expansion of which, designated retina, embraces the

refracting media of the eye like a cup, and is so fashioned as to be affected by the feeblest ray of light, and to transmit the impression then made upon it to the brain[666].

General Morphology of the Organ of Vision.

§ 312. The study of the eye in the animal kingdom, in reference to its progressive complexity of structure, is a subject of the highest physiological interest; inasmuch as we can here follow the successive steps that are taken from more simple to more compound structures. There are some animals, for example, among the infusories and medusæ, which have little pigmentary spots on certain parts of the body, that are regarded as rudiments of eyes; a proposition which can only be entertained as a problem, however, so long as no nerve can be demonstrated proceeding to these spots[667]. It is farther doubtful, whether those parts which in certain worms present themselves as enlargements upon the extremities of nerves, covered over with pigment, and having pupil-like apertures but no transparent refracting media in front of them, are to be considered as rudimentary eyes or not. Such organs could at best convey mere indefinite sensations of light and darkness. Wherever accurate observation conducts us, and we conclude from

[666] The works that treat of the phenomena of vision are very numerous; scarcely any other department of physiology has been so carefully cultivated as this. The special treatises of Porterfield, Schmidt, Brewster, Herschel, Kunzek, Goethe's *Farbenlehre, or Doctrine of Colours,* and the Elementary works of Biot, Pouillet, Arnott, Bird, &c., may be indicated. The illustrated works of Söemmerring and Arnold are universally known; and besides the usual elementary books on physiology, the recent treatises of Steinbuch, Müller, Purkinje, Tourtal, Treviranus, Volkmann, Heermann, Burow, and Szokalski, on the phenomena of vision generally, or more particularly, probably comprise all that is known on the subject. Particular treatises will be found especially referred to by and by, and there is much scattered material in the periodicals and yearly reports of Müller, Valentin, and Von Ammon. The excellent treatise of Ruete: *New Researches upon Squinting and its Treatment—Neue Untersuchungen ueber das Schielen,* &c., Gotting, 1841, requires separate mention in this place. It is the only one among the many works of recent date on squinting that has a physiological basis throughout, that gives genuine cases, and that shows the slightest advance in scientific ophthalmology.

[667] I cannot make up my mind to regard these pigmentary spots in the infusoria and medusæ as eyes. The coloured points discovered by Ehrenberg upon the extremities of the spines in the star-fishes, to which a minute nervous twig seems to be furnished, appear to have better claims to be so considered.

functional phenomena that the sense of proper vision is possessed, there do we find transparent media in front of a special apparatus; so that the eye of the very lowest animal already shows a certain degree of complexity. In the young of the medicinal leech, just escaped from the egg, a structure of this kind is demonstrable. Each of the six larger eyes receives a delicate nervous twig which proceeds under a reddish coloured pigmentary layer that surrounds, cup-wise, a transparent nucleus, corresponding to the vitreous humour and crystalline lens: this anteriorly is not obscured by any pigment, but like the pupil is open and permeable by the rays of light. In many of the marine-worms, Nereis and Lycoris, for example, we observe four ocular puncta. A considerable cerebral ganglion sends forward large nerves to the tentacula, and on either side two smaller branches to the eyes. If these eyes be gently compressed, the pigmentary cells that cover them separate, and a transparent centre comes into view[668]. More carefully studied, the anterior eye is seen surrounded by a transparent covering derived from the general envelope of the body, and the pigmentary layer is pierced by a pupillary aperture in front. The last part is wanting in the posterior eye; from both eyes, however, a round gelatinous and perfectly transparent mass escapes when the pigmentary layer is burst under the compressor. In these eyes, consequently, we have specimens of the simplest structures connected with a nervous expansion of the same nature as the retina in higher animals, and obviously calculated for distinct vision: A pupil receives the rays that are available for distinct vision, lateral rays being refused access by the pigmentary layer (the choroid coat and iris), whilst a transparent nucleus bespeaking the lens and vitreous body of higher animals effects the needful refractions of the luminous rays. The nerve appears to expand in the usual way into a cup-shaped retina[669].

§ 313. The more perfect articulated animals exhibit a similar but still more remarkable and complicated organization of the

[668] Müller maintains that in the Nereis these are mere papillary enlargements at the extremities of the optic nerves, without any dioptrical media. *Ann. des Sciences Nat.*, T. xxii. p. 19; vide also Rathke: *De Bopyro et Nereide*, Rigæ, 1827. All my more recent observations on annellidans permit me to suspect the presence of refringent media.

[669] The descriptions just given are from very recent and as yet unpublished observations made at Nice in the autumn of 1839.

organ of sight. First we have the simple eyes of the spiders and scorpions, in which there is a pretty thick cornea,—a transparent lamina of the general external integument; behind this there is a globular or elliptical crystalline lens; and farther, a peculiarly consistent vitreous body, which lies within the hollow of a cup-shaped retina; and this in its turn is surrounded by a pigmentary layer analogous to the tunica choroidea, which interposes between the lens and vitreous mass, but still leaves the centre free, whereby a pupil is fashioned which appears surrounded by a kind of iris[670]. Agreeing in all essential particulars of structure with this fixed eye of the arachnidans, is the moveable eye of the snails[671]. The compound eyes of insects seem to differ from them in nowise, save that many simple eyes are aggregated and very intimately connected. In this class there is a large, strongly arched, often hemispherical eye, the cornea of which is either uniform and smooth, or divided into a great number of four or six-sided fields or spaces (facets.) Each of these appears on a perpendicular section as a posteriorly greatly convex surface. Behind each of the facets of the cornea, there lies a conical or sugarloaf-shaped body, with the apex downwards or backwards,—the vitreous cone, which is a powerful dioptrical means, and corresponds to the vitreous body of the vertebrata. They are all sunk in a layer of pigment of various colours, which everywhere penetrates between them. Fine filaments of the optic nerve penetrate through the pigment, the optic nerve itself being an ample stem, proceeding by a broad and thick basis from the brain, and by and by dividing into a vast number of filaments, apparently primitive fibrils. Each of these filaments of the optic nerve penetrates to the apex of a vitreous cone, and expanding, surrounds it in the form of a disc-like retina[672]. The object of these mosaic-work eyes appears to be to supply the want of mobility: A fixed eye cannot be directed hither and thither; but a vaulted or hemispherical prominence

[670] Müller, *On the Comparative Physiology of the Sense of Vision—Zur Vergleichende Physiologie des Gesichtsinnes*, p. 315.

[671] My *Elements of Comparative Anatomy.* Figures in Müller's paper in the *Ann. des Sciences Nat.* vol. xxii, and Meckel's *Archiv*, 1829, Tab. vi.

[672] It would answer no end in this place were I to dilate upon all the varieties of compound eyes observed in insects and crustaceans. The subject has been lately very fully handled by Will in his *Contributions to the Anatomy of compound Eyes with facetted Corneæ—Beitraege zur Anatomie, &c.*, Leipz. 1840.

beset with eyes is fitted to receive rays from almost all sides, and so to admonish insects of the vicinity of their food or their enemies. The more convex the compound eye is, and the more numerous the facets upon its surface, as in the Libellulæ, the greater must the field of vision be, the greater must be the number of individual impressions made upon the optic nerve. The number of facets and vitreous cones generally amounts to a thousand, and more[673]. These compound eyes, moreover, do not require any of those changes in the relative position of the lens and retina, which are indispensable to secure equally perfect vision close at hand, and at a distance. Neither along with such a construction of eye have external media any influence; so that there is no difference in the structure of the eye in insects that live in air and in water[674].

§ 314. Throwing the lachrymal apparatus and external coverings of the eye out of consideration,—and these are all entirely accessory parts, in nowise immediately connected with vision,—we observe one uniform type in the structure of the eye in vertebrate animals, from man down to fishes. Wherever the eye is not imperfectly developed, as it is in the mole and myxine, it meets our observation as a hollow globe of considerable relative size, filled with refracting media, and having an elongated somewhat conical form, the apex of the cone being directed forwards and outwards, the base, inwards and backwards. This at least is the shape it presents in animals that live in air. In those that inhabit the water, the eyeball has more of a compressed rounded, or spheroidal form. The eyeball presents on its anterior aspect a circular transparent part, from the third to the fifth of its diameter in extent, which of course permits the access of light to the internal parts of the organ. Behind the transparent portion or cornea, but separated by the aqueous humour, lies the crystalline lens, a flattened biconcave body in animals that live in air, nearly a sphere in those that inhabit the water. Partly interposed between the crystalline lens and the cornea, floats the iris, a moveable circular diaphragm, capable of expanding and contracting, and so of increasing or diminishing

[673] In Musca domestic about 5000 may be reckoned, and in many butterflies, which are excellent subjects for observation, a still greater number. Vide Will, l. c. p. 11.

[674] Müller in his *Physiology* has given the subject of vision with compound eyes, like those of insects, very particular consideration.

its central aperture. The lens again is imbedded in the vitreous body or humour; and this in its turn is surrounded by the cup-shaped terminal expansion of the optic nerve,—the retina, which terminates anteriorly, behind the edge of the lens in a fine margin. Behind, and more externally than the retina, there is a thick pigmentary lamina, the six-sided cellular elements of which are filled with dark coloured molecules; and outside of this lies the choroid coat of the eye. The whole organ finally is enclosed within a dense fibrous tunic, which has often plates of bone deposited within it in the lower animals,—the sclerotic coat, the part that gives strength and consistence to the eye, and affords attachment to the anterior expansions of the muscles, by the combined actions of which it is endowed with a very delicate and complete system of motions.[675].

Structure and Functions of the several parts of the Eye.

§ 315. Eyes provided with collective dioptrical media, (§ 314,) differ from the compound tessellated eyes of insects (§ 313), in which the whole of the luminous rays that impinge upon the cornea are also conducted to the retina. In man and the vertebrata, but a relatively small segment of the cornea permits the admission of the rays of light. Rays that impinge upon the cornea at a less angle than 48°, are, however, still so much refracted, that they find entrance into the eye. In man the refracting power of the cornea is everywhere very much alike, whether at the side or in the middle, inasmuch as it is everywhere of equal thickness, and its two surfaces are concentric or parallel[676]. To have a sufficiently ample field for ordinary vision, the eyelids require to be so far apart as to expose the whole surface of the cornea,

[675] Greater details will be found in works on human and comparative anatomy. W. Söemmerring takes a very interesting survey of the structure of the eye in the vertebrate series of animals, in his work, *De Oculorum Sectione Horizontali.* Tab. ii. and iii. [See also Wharton Jones' horizontal section and description of the eye, in Mackenzie's *Practical Treatise on the Diseases of the Eye,* 3d ed, 1840, in which the whole physiology of the eye is treated with the greatest perspicuity. R. W.]

[676] The cornea varies greatly in thickness, both generally and with reference to its particular parts. In fishes it is much thicker around the margin than in the middle.

and this they are generally. Any opacity in the cornea of course impedes, in proportion to its extent, the access of luminous rays to the eye, and so interferes with vision. The great brilliancy of the surface of the cornea, which gives the eye its lustre, causes a certain number of luminous rays to be reflected from it, and renders it a mirror of external objects, in harmony with the laws of catoptrics[677].

§ 316. The AQUEOUS HUMOUR appears to serve partly as a refracting medium, and partly as a means of giving form to the anterior portion of the eye. The degree of convexity of the cornea, which varies both in tribes and individuals, would seem to be closely connected with the quantity of the aqueous humour[678]. The aqueous humour occupying both the anterior and posterior chamber of the eye, also enables the IRIS to enjoy perfect freedom of motion. The iris performs precisely the same office as the diaphragms of our optical instruments, which we introduce to correct, or rather to prevent, the indistinctness of vision which arises from the spherical aberration of our lenses. By shading the sides of the crystalline lens, the iris hinders all but those rays which fall perpendicularly upon its middle, from entering the eye. The diameter of the pupil, however, varies continually, in harmony with the number and intensity of the luminous rays that impinge upon the cornea; and this it does involuntarily, in virtue of a wonderful inherent power, connected with a peculiar nervous susceptibility, by which the degree of contraction or relaxation necessary to the most perfect vision is secured. In ordinary day-light, and in the shade, the iris generally remains steady; with varying intensities of light it becomes broader or narrower. The greater the light the narrower is the pupil; the weaker the light, the wider does the pupil become; and this is obviously in the one case to admit a smaller, in the other a larger amount of luminous rays. But, more than this, it is found

677 For information on the intimate structure of the cornea, consult the elementary works on anatomy and histology, particularly Henle's *General Anat.* p. 320.

678 The very remarkable convexity of the cornea in the birds of prey generally, and the abundance of the aqueous humour, seem to stand to each other in the relation of cause and effect. [It would probably be more correct to say that they were intimately associated, or even necessarily connected, than that the one was the cause of the other. The grand office of the aqueous humour is to facilitate the motions of the iris. R. W.]

that the nearer the object is which we contemplate, the narrower is the pupil; the more remote the object, the wider is the pupil. Still farther, the more intently we regard an object close at hand, the narrower does the inlet to the luminous rays become. In harmony with the laws of optics, from the influence of no one of which is the eye abstracted, we see most distinctly when the pupil is small, the object as understood being at the proper distance for distinct vision, and duly illuminated; all disturbing marginal rays are then excluded. The posterior dark surface of the iris (Uvea) serves for the absorption of rays reflected from one part to another in the interior of the eye. As all the motions of the two eyes are harmonious, so the pupils dilate and contract in unison. The motions of the iris are of the kind called reflex; that is to say, they follow automatically from stimulation of the retina, which transmits impressions made upon it through the optic nerve to the brain and medulla oblongata, whence they are communicated to the third pair, the nerve that supplies branches to the iris (§ 248). The pupil is fixed and motionless in amaurosis, in which the optic nerve has lost its sensibility and power of conducting impressions. The iris, however, is affected under a great variety of physiological and pathological conditions; and several narcotic substances, belladonna in particular, have a peculiar influence upon its motions.[679]

§ 317. The CRYSTALLINE LENS is the most important refracting medium of the eye. It presents a very great variety of forms in the class of vertebrate animals, and is by so much the more dense in its structure, and convex in its form, as there is less difference between it and the medium wherein the life of the animal in which it is examined is passed. Fishes and quadrupeds have for the most part a flattish cornea, and a nearly spherical crystalline lens. In man the lens is biconvex. Its structure, and the form of its surfaces, are such, that in refracting it still preserves the ray of light in its perfectly achromatic state. The lens is inclosed in a particular capsule, a perfectly transparent, structureless and vesselless

679 In birds, among which the iris is moveable at will, I have satisfied myself that the fibres which proceed to it from the ligamentum ciliare have the histological character of the voluntary muscles generally, viz. the characteristic transverse striæ. In man and the mammalia the iris, to all appearance, consists entirely of fibres of cellular membrane. Vide Henle, *Op. Cit.* p. 574. He, however, regards it as composed of muscular fibres, having the character of the fibres of cellular tissue. [See the description of the eye by W. Jones in Mackenzie, (§ 19.) R. W.]

membrane[680]. In this capsule it appears to lie free, connected with it anteriorly and posteriorly, however, by means of a clear, somewhat viscid fluid, the liquor Morgagni of anatomists, which contains numbers of spindle-shape, extremely delicate, perfectly transparent nucleated cells[681]. As the surface of the lens exhibits cells precisely of the same description, we may presume that betwixt the lens and its capsule, there is an uniform very delicate stratum of cells interposed. Under these cells we encounter fibrous layers, which form concentric laminæ, like those of an onion, around the nucleus of the lens. In the lens hardened by maceration in alcohol, these layers peel off quite regularly. If we suppose a line to be drawn from before backwards, through the centre of the lens as an axis, and the polar circumference of the body be compared with its æquator, the fibres will be found to pass like meridian lines through the poles to the æquator. The constituent fibres themselves have a crystalline six-sided figure; and the surface of a section of the lens which passes perpendicularly through a bundle of such fibres presents a mosaic or pavement-like appearance. In fishes, the fibres of the lens are toothed at the edges; and here, like the bones of the skull, they indent each other and form sutures[682]. In the periphery of the lens the fibres united into plates, in the manner described, are connected together by means of a soft amorphous matter. Towards the centre of the body this matter is wanting, so that there the fibres lie closer, and form the denser nucleus. The anterior surface of the human crystalline lens is flatter, and its curve forms a portion of an ellipse; the posterior surface, which is sunk within a corresponding pit or depression of the vitreous substance, is more curved, and of

680 Henle is disposed to regard the capsule of the lens and other similar parts as members of a particular system of organic tissues, which may be spoken of under the generic title of *hyaline* membranes or tissues; *Allgem. Anat.* S. 327; [Gerber, (Valentin?) has spoken at large upon this subject, and had already taken a similar view. *General Anatomy, with appendix and notes* by Gulliver. R. W.]

681 Upon this very delicate structure, as well as upon every thing else appertaining to the histology of the crystalline lens, see the admirable work of Werneck: *Contributions to the histology of the crystalline lens—Beiträge zur Gewebslehre des Krystallkoerpers*, in Von Ammon's *Zeitschrift*, B. v. S. 403; also Henle, l. c. Tab. ii. Fig. ii.

682 Consult the numerous and extensive observations of Werneck, l. c., and farther, the excellent paper of Dr. Brewster, in *Philos. Trans.*, 1836.

a parabolic figure[683]. The whole structure of the lens harmonizes wonderfully with all that theory and experience demonstrate as the best for biconvex lenses; it may be viewed as a biconvex lens so fashioned as to lessen in the greatest possible degree, or even entirely to do away with, spherical and chromatic aberrations. The iris, by shutting out all lateral rays, must aid in this in no inconsiderable degree; but the lens has a means of correction within itself, which probably makes it independent of the iris, and which is unapproached and unapproachable in any instrument produced by art, viz. a progressively increasing refringent power, by a progressively increasing density, from the circumference to the centre. In our optical instruments we do all we can by grinding the opposite surfaces of our lenses to different curves, and by associating lenses made of glass having different refracting powers (crown and flint glass), to prevent the aberrations from sphericity and unequal refrangibility in the rays of the spectrum, but the best we can accomplish falls infinitely short of what nature has effected in ordering the structure of the crystalline lens of the eye as she has done. The curious construction of the lens from fibres must also, beyond all question, exert an influence on the refraction of the rays of light, the nature of which, however, is at present unknown to us. Pathological occurrences seem to assure us of this; for clefts occurring between the layers of fibres composing the lens, cause manifold refractions, and present the individual with a corresponding number of images of the same object[684].

683 These facts from the measurements of Krause, *Elemts. of Anat.* 2d ed., 1842. p. 541, whose account of the structure of the eye is particularly to be commended. He found the anterior surface of the lens to have an elliptical curve, whose long axis varied, in different cases from 4''' to $5\frac{1}{10}$''', and whose short axis varied in like manner, from $1\frac{2}{3}$''' to $2\frac{1}{4}$'''.—The posterior surface had a parabolic curve, whose parameter was from $3\frac{4}{5}$''' to 5'''.

684 Professor Ruete communicated an extremely interesting case to me of this kind. A man, 62 years of age, who suffered with his eyes, was astonished to find on looking at the moon from his chamber, that she presented no fewer than twelve distinct discs; this was the case in both eyes. The twelve clear images appeared regularly, at equal distances, disposed in a circle around a dark disc, like a rosette with a dark centre. Other clear bodies, such as a taper, the bulb of a thermometer at the distance of fifteen feet he saw multiplied to the same degree; objects viewed close to the eye were seen single. On looking into the eyes through the pupil, a tangled net of white streaks is perceived. The explanation of the phenomenon observed in this case is difficult; it might perhaps be fairly

§ 318. Among the transparent media of the eye, a very important one is the VITREOUS BODY. It consists principally of a limpid, slightly albuminous fluid—the vitreous humour, which is contained in a multitude of small cells, processes of the membrane which surrounds the body generally—the tunica hyaloidea. Anteriorly the vitreous mass is depressed for the reception of the crystalline lens, posteriorly it is rounded; it is therefore comparable to a very thick convexo-concave lens, for its antero-posterior diameter measures as many as nine lines. The vitreous body keeps the retina expanded; if by any accident it escapes, as it does by wounds, and as it frequently has done during operation for the extraction of a cataract, the retina collapses, and vision is immediately lost. Opacities in the vitreous body, slight flocculent precipitates within its substance, etc. give rise to subjective visual phenomena, for example to muscæ volitantes, and other figures of more definite form moving before the eyes. Similar phenomena arise when in consequence of congestion or inflammation, the extremely minute blood vessels of the vitreous body, which generally admit few or no red particles, come to be loaded with these[685]. Total blindness may ensue from changes in the nature and constitution of the vitreous body; the consequences of such changes are those opacities and hazinesses that are particularly designated under the titles of Glaucoma, Synchesis, etc. diseases in

brought into juxtaposition with the experiment of Scheiner, (§ 330,) unless we would refer it to a multiplied refraction of the luminous rays effected by different bundles of the lenticular fibres, so that the lens in this instance was brought to resemble the eye of an insect (§ 313) furnished with twelve crystalline cones. [In looking at the half-moon without my spectacles, I see a large disc, which I can make out to be made up of about a dozen half-moons, lying one over the other in a circle, as it appears. R. W.]

685 The latest observers are somewhat unanimous upon the presence of blood-vessels in the vitreous body; these may be filled by forced injections; but they are probably too delicate to admit blood-discs in the natural state. Krause says, (*Op. Cit.*, p. 540.) the tunica hyaloidea possesses highly delicate blood-vessels, which, by reason of their tenuity, admit no blood-discs in adults. These vessels are derived from the arteria centralis retinæ, and expand themselves partly on the outer envelope of the vitreous body; but a larger branch passes forwards through the middle of the vitreous body, which gives off twigs laterally to the walls of the cells, and terminates on the posterior wall of the capsule of the lens. [The freedom with which the posterior segment of the capsule of the lens is supplied with blood-vessels, when contrasted with the absolute freedom from vessels of the anterior segment of the same part, is very remarkable. R. W.]

connection with which we are still in want of a searching anatomical and physiological examination of phenomena and structural alterations[686].

§ 319. The membraniform expansion of the optic nerve,—the RETINA, surrounds the vitreous body immediately. It consists of several layers, the intimate structure and stratification of which belong to the most difficult subjects of microscopical investigation[687]. It is absolutely necessary that we undertake a new and more careful examination of this part; for it is really important in the explanation of various phenomena of vision. The human eye, unfortunately, is seldom or never a good subject for studying the retina; for we can scarcely procure it in so recent a state as permits us to observe any of the more delicate points in the structure of its parts. We therefore have recourse to the perfectly fresh eyes of animals just killed; for example, to the eyes of rabbits[688]. Here we find no difficulty in observing the primitive fibrils of the optic nerve, immediately after their passage through the sclerotic coat, separating into tufts like those of a sprinkling brush, and advancing in fasciculi, which form plexiform groups. Betwixt the several bundles of pri-

686 [The appearance of opacity in Glaucoma depends on a reflection of light from the bottom of the eye, connected with a diminution of pigment and a morbidly opaque state of the retina. There is usually also some degree of opacity of the lens which influences the glaucomatous appearance. But more than this, there are always in such cases co-existent changes to a greater or less amount in the retina. R. W.]

687 I have given the description in the text principally from individual observations, which agree in the main with those of Henle and of Krause. Besides the writings of these two excellent observers, we have several papers and monographies, particularly that of Valentin in his *Repertorium*, (1837, p. 250,) and that of Hannover in Müller's *Archiv*, (1840, p. 320). The numerous and unhappily so often contradictory labours of the last few years, (by Ehrenberg, Treviranus, Gottsche, Remak, Bidder, &c.,) on the structure of the retina, may be found referred to by Krause, (p. 739,) and Henle, (p. 774).

688 The retina must be examined in the freshest possible state, and immediately after death; I particularly recommend white rabbits as subjects, the pigmentary matter of the choroid coat presenting no obstacle to observation. It is desirable, however, at the same time, to have several subjects at hand for comparative examination,—birds, fishes, frogs, as in them some of the structures, particularly the columnar layer, is larger and more distinct than usual. The paper of Hannover, above cited, is very much to be recommended as a guide in this difficult investigation. Pressure and much manipulation are very objectionable, although the weight of a plate of thin glass is very well borne.

mitive fibrils, fusiform spaces are left free. The primitive fibrils are excessively fine, partly cylindrical, partly varicose, and very similar to the medullary fibres of the brain (§ 231). They are from $\frac{1}{600}$th to $\frac{1}{800}$th of a line in diameter. It is altogether unknown how they comport themselves further on in their course; for they soon escape observation, although single fibrillæ may still be indistinctly traced to the anterior margin of the retina. Loop-like terminations, which have been described by some observers, can never be clearly made out[689]. This layer of primitive fibrils constitutes the middle element of the retina, and is called the stratum fibrillosum[690].

Externally from this, there is a second layer, which appears composed of little columns or cylinders—the stratum bacillosum s. cylindrosum. This columnar layer is covered on the outer aspect with pigmentary matter. It appears to be made up of an aggregation of rounded, or, by consequence of mutual pressure, prismatic columns, about $\frac{1}{100}$th of a line in length, and $\frac{1}{600}$th or $\frac{1}{800}$th of a line in thickness. Considered on its outer or choroidal aspect, it has all the characters of a piece of mosaic work or fine pavement. The little columns are readily detached, and then float about in the field as small isolated, transparent and rigid bodies, slightly bent at one end. They become variously bent by the action of water. In a fluid they exhibit molecular movements. This columnar structure is obviously to be regarded as a peculiar apparatus set perpendicular upon, but not in anatomical continuity with, the primitive fibrils of the stratum fibrillosum[691].

The third or inner layer of the retina—the stratum globulosum s. cellulosum—is the most difficult of all to study. It consists of a

689 I have not myself, any more than Hannover, succeeded in making out the terminal loopings of the primitive fibrils of the retina, which are nevertheless described by Krause, and admitted by Valentin as extremely probable.

690 I have here followed the terminology of Krause, which appears extremely well chosen.

691 I believe that I was the first to describe these bacilli, or little columns of the retina, as a particular structure; (Burdach's *Physiology*, v. 143). It was long a subject of dispute whether the layer lay inwardly from that of the primitive fibrils, or outwardly, which is now the generally received and true view. (Vide Henle, *Allg. Anat.* S. 783.) It has been described as a particular membrane, under the name of membrana Jacobi. This membrane, as it was demonstrated by Dr. Jacob, appears to be the stratum bacillosum, very much altered by the action of water.

congeries of extremely pale, delicate, nucleated cells, which form a double or multiple layer, interposed between the fibrillæ of the stratum bacillosum and the vitreous body. By some this layer has been referred to the cellular epithelial formations; by others it has been viewed as a stratum of ganglionic corpuscles[692].

Exactly in the axis of the eye, a little to the outside of the point of entrance of the optic nerve, we observe the limbus luteus,—a pale yellow-coloured oval spot about a line in diameter. Microscopically considered, it is found to be formed by a gap among the primitive fibrils—it is a mesh of unusual size in the nervous network, and the fibrils appear piled up around it. The fibrillous layer is consequently wanting over the macula lutea, but the columnar stratum is present, about 600 of its columns corresponding to the space occupied by the spot. The rays which strike through the axis of the eye in ordinary vision, by which the most sharply defined and distinct images are formed, fall directly upon the limbus luteus[693].

692 Valentin regards these cells as identical with the ganglionic corpuscles, and Hannover speaks of them under the title of cerebral cells. Valentin recognizes a double layer of cells: — immediately on the primitive fibrils, a layer of nuclear globules, over which lies an inner and pale cellular layer. Krause is extremely minute in his description, and distinguishes two layers of cells, one considerably larger than the other; he thinks that, in all probability, they are ganglionic corpuscles (l. c. p. 538.) To myself, the nature of this cellular layer—this stratum globulosum—has always appeared extremely doubtful, in the same way as the corresponding structure in the labyrinth (§ 307). It strikes me that the new views of Henle are far more likely to be found correct. Henle conceives that the globules of the retina are by no means identical with the proper ganglionic corpuscles of the brain, particles with which they have nothing more in common than general structure, which belongs alike to all the cellular elements of organized bodies. In form, size, and chemical relations they differ entirely; they are, in fact, much more analogous to the cells of the outer lamina of the crystalline lens; and this led to the idea that perchance they belonged in fact to the transparent parts of the eye, that they constituted a kind of epithelium or rete Malpighii, covering the nervous fibrils, and supporting them in their expansion, &c. In this way the more internal layer of cells would very naturally correspond with the fully ripe or flattening layer of epithelial cells, the more external layer, again, would answer to the younger nucleated cells of epithelial structures generally.

693 The description of Krause appears to me to agree best with nature here. The foramen of Söemmerring with its limbus luteus requires renewed and careful study; the eyes of monkeys immediately after death would probably afford the best subjects for observation, these being the only animals in which the part

The blood-vessels of the retina are distributed upon its internal aspect, or that which is turned towards the vitreous body, betwixt the different strata of cells, and form with this what has been called the vascular lamina.

§ 320. From the difficulties experienced in determining the functional significance of the several layers of the retina, it comes to be a point of more than usual interest to trace their connection with the central parts of the nervous system, and particularly to study the development of the eye in its earliest stages. We have already seen (§ 55) that the eye is formed by evolution from the middle (in the beginning it is the first, and only by and by the second or middle) cerebral cell. This point is very beautifully seen in the chick at the end of the second day, about the 48th or 50th hour of the incubation. The evolution here proceeds with great rapidity; the embryo is now in shape, something like a hammer; under the influence of a rapid formative nisus, conical enlargements arise on either side, which push the bounding vertebral laminæ outwards. The outermost arched portions form the vesicle of the retina, which is soon filled with the vitreous humour, and is by this time pinched off from the middle cerebral cell. The optic nerve is produced betwcen the two, in the form of a tube, which communicates freely with the brain, and retinal sac; in the embryo, both of man and animals, it long continues tubular. By and by the two eyes diverge to either side, and the optic nerves blend towards the middle line in the commissure or chiasma, which for a time stands as a kind of boundary betwixt the brain and the eye. During these histological changes, the chiasma and optic nerve become filled with fibrils, which, united into fasciculi, partially decussate, so that several of the bundles of the left optic nerve proceed to the right tractus opticus and thalamus, and vice versa; an anatomical fact by which the physiological consequences immediately to be described, are readily explicable. In the chiasma, we discover nothing like ganglionic corpuscles, a circumstance which makes it all the less likely that any should be evolved upon the retina or peripheral expansion of the nerve; it may be said, indeed, that ganglionic globules are

occurs except man. It appears to be in some way connected with the parallelism of the axes of the eyes. Vide Ammon, *De genesi et usu maculæ luteæ in retina oculi humani obviæ*, Vimar. 1830.

no where to be certainly detected, in connection with the terminations of the nerves of sense.

General analogy leads us to regard the fibrillous layer both as the recipient of the impression, and the apparatus of conduction. It is so spread out, that every individual fibril must receive the impression of luminous rays throughout its entire length, and not at its extremity only. The impression here must, we should presume from the anatomical structure, be made by the direct rays, which through the vitreous body and the cellular lamina fall upon the primitive fibrils. Wherever these last are overlaid by vessels, no distinct impression is made[694]. Beyond all question, the never-failing stratum bacillosum must also exert an important influence upon vision; but of the absolute nature of its action or office we are left to conjecture. That the bacilli themselves constitute a sensitive nervous apparatus is extremely improbable; they are not in anatomical connection with the primitive fibrils[695]; it would also be against all analogy were we to admit a peculiar nervous substance, met with in no other situation, and altogether different in its character from every other form of nervous substance known. The structure of the columnar lamina seems rather to point it out as a peculiar optical (dioptrical?) apparatus, associated with the most delicate percipience of the luminous rays; perhaps it is an apparatus of reflection, destined to convey to the primitive fibrils excessively delicate and isolated impressions, it may be in something of the same way as the otolithes of the acoustic apparatus, and farther, to influence the quality of the images, and to assist in the discrimination of colours[696]. The presence of the columnar lamina at the foramen of Soemmerring, the very point where we see best, and the fencing in or circumvallation of this aperture by the primitive fibrils, seem to give us further assurance of these surmises being well founded.

The visual perception of objects depends on the integrity of the retina; if it be dynamically or materially injured or destroyed,

694 Vide farther under § 340 on the optical spectrum in the eye.

695 According to the ideas of Treviranus, Henle, and others, which at one time were very extensively accredited, but are now no longer regarded, the primitive fibrillæ bent round immediately into the bacilli, the extremities of which were then held to represent the papillæ of the nervous primitive fibrils.

696 Hypothetical notions which will be again passed in review when we come to speak of the phenomena of vision.

if its state of due distension be disturbed by the discharge of the vitreous humour, if it be cut off from its continuity with the optic nerve, etc., amaurosis or blindness from paralysis of the nervous apparatus is the consequence[697].

§ 321. The CHOROID COAT of the eye is a delicate membrane, constituted almost entirely of a vascular rete, upon the internal aspect or surface of which, as also upon the posterior aspect of the iris, there is an intensely black layer of pigmentary matter deposited. This pigmentary matter consists of an aggregation of three, four, six, and many sided corpuscles, which exhibit the cellular type in great perfection: In the centre they contain a clear nucleus, and their periphery is constituted by a most delicate membrane, which includes a quantity of dark-coloured molecules as contents. In cases where the pigmentary matter is wanting, as it is in leucœthiopic men and animals, we find cells only,—delicate transparent envelopes, without any pigmentary deposit in their interior. Albinos have red pupils, as is well known, from there being no absorption of the rays of light that penetrate the eye; on the contrary, the rays are reflected backwards and forwards, so that the eye is illuminated throughout, and the vascular rete of the choroid, of the retina and of the iris are perceived shining through. Individuals of this kind are fearful of the bright light of day; they only see well in moderate degrees of light, in the twilight, for instance. In the sunshine and bright light, they are in fact dazzled by the rays of light that are reflected from every surface in the interior of the globe of the eye. The obvious business of the pigmentum nigrum is therefore to absorb the rays of light so soon as they have done their business upon the retina, and so prevent them from being reflected a second time, and thus disturbing the accuracy of outline of the images formed upon it. We always make use of a dead black pigment to cover the inner surface and diaphragms of our optical instruments. The great vascularity of the choroid coat may be for the purpose of enabling it to secrete the pigment abundantly; perhaps also its object is to maintain the temperature of the eye at the proper pitch; and then

697 It is much to be regretted that all the anatomical examinations of amaurotic eyes which have hitherto been made, from their want of microscopical details, should be without any value; nevertheless morbid anatomical facts might here prove of signal value in clearing up the physiological meaning of the different layers of the retina.

all organs entrusted with important functions, and having an abundance of nerves distributed to them, seem to require a large supply of blood.

§ 322. The external parts of the eye—eye-lids, eye-brows, and conjunctiva—are mere supplementary or defensive pieces of apparatus, which, however, are not without their influence upon vision. The eye-brows, spanned upon bony ridges of corresponding form, shade the eyes from the generally intense luminous rays which strike perpendicularly from above, etc. The eye-lids have also the same among other important offices, such as distributing the fluid that keeps the surface of the cornea constantly moist and brilliant, protecting the eye-ball during sleep, etc[698].

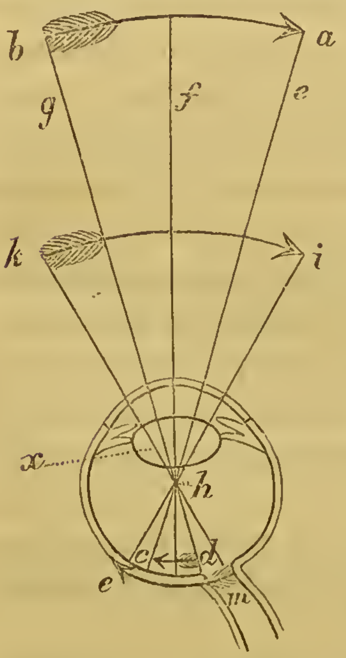
Dioptrics of the Human Eye.

§ 323. The rays of light which attain the retina and there unite to form images, must of course pass through the whole of the refracting media described in the preceding paragraphs. The refracting powers of these media, which are spoken of collectively as the humours of the eye, differ in conformity with the fashion, structure, density, and chemical constitution of each[699]. These humours are farther the principal cause of the form of the eye-ball, which not only differs in reference to kinds, but also among individuals of the same kind. In man, the eye-ball, in a general way, presents the form of an ellipsoid open in front, where it is met and completed by a small segment of a sphere engrafted upon it. The axis of the eye corresponds with the optic or visual axis, and extends from the centre of the cornea backwards to the foramen of Soemmerring, a little to the outside of the point at which the optic nerve makes its entrance. This optic axis of the eye measures on an average from 10½ to 11 lines, and differs from the axis of the optic nerve

[698] The teleology—or doctrine of the ends answered by the accessory apparatus of the eye,—is treated of at great length by Arnold in his *Physiology*, (§ 695.)

[699] We have various estimates of the refracting powers of the transparent media of the eye, a summary of which is given by Weber in his Edition of Hildebrand's *Anatomy*, IV. 103. The numbers of the several humours of the human eye, according to Brewster, are the following: Cornea 1,386; aqueous humour 1,3366; lens as a whole 1,3767; middle portion of the same 1,3786; nucleus of ditto 1,3999 (according to Young 1,4025); vitreous humour 1,3394.

which passes from the outer third of the cornea, to the middle of the point of entrance of the optic nerve, crossing the optic axis at an angle of about 20 degrees[700]. In its general condition, the eye is so fashioned that the rays which arrive from a point divergingly upon the cornea, are immediately made to converge, and this in such measure precisely, that they meet in a focus as they attain the retina. It is of course the central ray alone of a pencil of rays, that passes through dioptric media unrefracted; all the other rays suffer refraction, and are approximated to the central ray. The rays composing a pencil falling upon the cornea are refracted in different degrees by the transparent media of the eye, in proportion to the difference between the density of these media and that of the air, and in proportion to the curves presented by their several surfaces. The rays are in the first place refracted by the cornea, by the membrane of the aqueous humour, and by the aqueous humour itself; then, and very particularly, by the crystalline lens, and that differently, by different strata of this body in the ratio of their several densities (§ 317); finally, by the vitreous humour; having passed through which they have come to a focus, and reached the retina at one and the same moment.



§ 324. When the object from which the rays of light proceed has extent in space,—length and breadth, suppose, for example, that it is the arrow *a*, *b*, in the accompanying diagram,—then must the object of necessity appear reversed upon the retina *c*, *d*; that which is superior in the object becomes inferior, that which is to the right appears to the left in the image[701]. As every object emits rays from every point in all directions, which then proceed in straight lines, the axal rays *e*, *f*, *g*, of the different pencils proceeding from either end, and the middle of the arrow, *a*, *b*, must cross at some point within the eye. Nu-

700 I have followed Krause here, whose measurements appear to me accurate. See his *Anatomy*, 2d Ed., and also his previous paper *On the structure and dimensions of the Human Eye* in Meekel's Archiv, 1832.

701 It is most easy to obtain conviction of this reversed position of objects upon the retina, by taking the eye of a white rabbit, free from pigment, clearing

merous observations satisfy us that this point lies very near the centre of the eye, (h,) somewhat behind the crystalline lens, (x). The prime rays, e, f, g, which proceed from the object may be named, in reference to the eye, rays of direction, because every prime or axal ray of a pencil determines the direction of the other rays, in order that all of them may meet in a focus upon the retina. The point at which the rays must diverge, if a clearly defined image is to be formed, is called the point of intersection or focal centre[702]. The position of this point is determinable with the assistance of an instrument for measuring angles; it lies somewhat behind the crystalline lens, and very near the centre of the eye. The intersecting axal rays of two objective points inclose an angle (a, h, b, for the object, a, b; i, k, h, for the object i, k), which is called the visual angle. This angle diminishes with the distance of the two objects from the eye, and the retinal image is in the same proportion smaller. The arrow, i, k, is only half the distance of the arrow a, b, from the eye; the visual angle, i, h, k, is therefore twice as large as the angle, a, h, b, and the same thing is true in reference to the images depicted upon the retina.

the globe from fat, muscles, &c., and then presenting it with the cornea in front to the window; all the objects before it, such as trees, houses, &c., are perceived forming a very elegant little picture, but reversed or upside down upon the posterior wall of the transparent eye. If a simple or double glass lens be now placed at a proper distance, the reversed image which the objects refracted by the crystalline lens form, may be projected on a sheet of paper.

702 Volkmann instituted many very able experiments upon the condition of retinal images, and from this inferred the focal centre. An experiment easily performed is the following. Upon an horizontal table let a number of straight lines $a\ a'$, $b\ b'$, &c., be drawn, all of which intersect at the point c; upon this point, c, let a prepared white rabbit's eye, E, Y, E, be so placed, that the axis of the eye coincides with the line d, d'. If the anterior part of the cornea, Y, stand at the due distance from c, then will objects at a, b, d, e, f, form their appropriate retinal images, at a'', b'', d'', e'', f''. The chamber being darkened, let tapers be placed at a, b, d, e, f, and the spectator look successively at a, from a', at b, from b', at d, from d', &c., and it will be found that the line of vision will cut the retinal image of a, at a'', of b, at b'', &c. The retinal images of the whole of the tapers lie in straight lines, which intersect at the focal point, c.

It is on this account that objects of different magnitudes seen at different distances, but of which the visual angles are the same, form retinal images of the same size[703].

§ 325. All images falling upon the retina through the dioptrical media of the eye are appreciated, but all are not seen with equal distinctness. Images appear by so much the more indistinct, as they are formed more remotely from the point upon which the optic axis of the eye falls (§ 322). This point corresponds very accurately to the foramen of Soemmerring[704]. Whether the peculiar distinctness of vision at this point depends on the structure of the retina there, or is to be ascribed to this, that in the usual position of the eyes, their axes are so directed towards objects, that the principal rays from these strike through the centres of the lenses, remains doubtful. The latter view is however the more probable[705]. For as those

[703] This is very readily demonstrated practically, by means of the arrangement indicated in Annot. 100, the window-frame is aptly made the term of comparison between objects either nearer or more remote.

[704] The observations of Herschel and other astronomers show, however, that with reference to objects at an extremely great distance, vision is not the most perfect when the image falls upon the retina in the optic axis; but upon a point within a small circle around it. This can be best determined by selecting on a fine star-light night a small star, with another scarcely visible star close beside it, for observation. If the eye be now directed to one of these stars, it forthwith becomes less bright and distinct than it was whilst the other was particularly regarded; in short, the object is not seen to most advantage by being looked at directly, but when a point at some very short distance from it is fixed in the optic axis. Some very minute stars are in fact lost sight of altogether when we seek to fix them; but as the eye travels to the side of them, they start out of the darkness very distinctly. Vide Herschel, in *Philos. Trans.*, and Ruete's work *On Squinting*. I cannot confirm Herschel's views from personal experience, for which indeed we should feel at a loss to assign any reason, either physiological or physical. [There is probably some peculiarity in the eyes of certain persons that causes the effect described by Sir John Herschel. I remember very well to have observed the phenomenon he describes in former years, and to have been very much puzzled with it. Is it connected with the imperfection of eye which induces short-sightedness? R. W.]

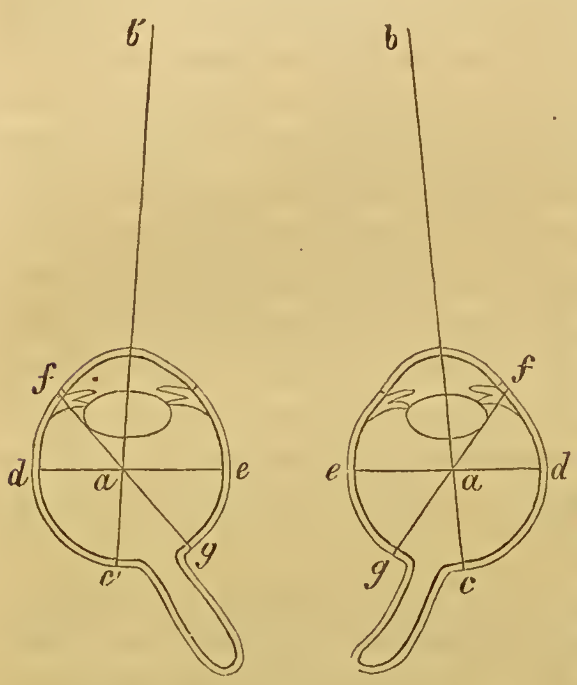
[705] It appears to me far more likely that the more definite vision is connected with the latter circumstance. The limbus luteus is perchance rather a consequence than a cause of vision in this point. Animals in which the limbus luteus is wanting, still enjoy a very keen sight; the fishing eagle pounces from a very great height, with unerring precision, upon the fish, which he can only have seen as a very small object from his elevated position. The same thing is true in regard to many other birds, and to animals in general.

rays of a pencil of light that strike through the edges of the lens must be differently refracted from those that pass through its centre; in consequence of the difference of density between these edges and the centre, etc., they cannot all unite in the same focus; hence there is unequal dispersion and ill defined images. And it is not unimportant to observe, that we do not in fact see more than a single point of an object with perfect distinctness; if we seem to take in more, it is only from the rapidity with which the eyes travel and survey each point in succession one after the other. In surveying a picture closely, we are conscious of this—we look at one part after another; at a distance indeed, we receive a general impression of the work, but this is only because the rays then come from the object at large in a pencil so delicate, that it passes entirely by the centre of the lens. There is a particular circumscribed spot at the bottom of the eye, corresponding to the place of entrance of the optic nerve, or at all events to the centre of this part which the arteria centralis retinæ perforates, where we have no sense of visual perception[706].

§ 326. The motions of the eye are of great importance in the act of vision. As in the steady contemplation of objects we have to bring them into the focal centre of the produced visual axis, we necessarily move the eye-ball in the act of looking around and

[706] Marrotti was the first who described the disappearance of the visual image at the entrance point of the optic nerve. To make the experiment, let two black objects be taken and placed at *a*, and *b*, upon a white ground. From the diagram it is seen that in the right eye, the spot, *a*, falls upon the point of the retina, *a'*, whilst the cross, *b*, falls in the middle of the entrance point of the optic nerve, precisely where the central artery and vein of the retina are situated. Now if the left eye be closed, and the point *a*, and cross *b*, are regarded at the usual distance for distinct vision, the attention being, however, particularly directed to *a*, the cross *b* will be found to disappear the moment the pencil of rays proceeding from it comes to fall upon the middle of the entrance place of the optic nerve.

studying the details of objects successively, according to determinate laws. It has been ascertained that in this motion the eye-ball revolves accurately round a point,—the point of revolution of the eye—which remains unaltered; it is at once the point of intersection of the rays of direction and of those of vision (§ 324). In this



point, *a*, in the appended diagram, all the diameters of the eye intersect, and many of these diameters are at the same time the axes of revolution with reference to the actions of the muscles of the eye. If the two eyes be directed to the points *b* and *b'*, the axal rays fall upon *c* and *c'*. Both eyes then look forwards, and also somewhat convergingly, so that the two axes *b c*, and *b' c'*, do not run precisely parallel, but diverge slightly, by which *c* and *c'* are further from one another than *b* and *b'*. In the horizontal transverse diameter *d e*, which runs from the temporal to the nasal side of the eye-ball, lies the axis of the organ in reference to the action of the superior and inferior straight muscles. The perpendicular diameter passes from above downwards through the point of revolution *a*, cutting the transverse diameter at a right angle, and is at the same time the axis of revolution of the internal and external straight muscles of the eye. A line drawn from the outer margin of the cornea, *f*, to the inside of the entrance place of the optic nerve, *g*, represents the horizontal diagonal axis of the eye-ball, and is at the same time the axis of revolution in reference to the two oblique muscles. The superior oblique turns the pupil downwards and outwards; the inferior oblique turns it upwards and outwards. The action of the whole muscles of the eye is productive of no change in the position of the eye-ball, but only of a revolution upon its axis[707].

[707] On the revolution-point of the eye, vide Volkmann, l. c. p. 34. On the action of the muscles of the eye, the work of Hueck: *The motions of the Eye round its axis—Die Achsendrehung des Auges*, Dorpat, 1838; and also the

§ 327. The eye moves around the several axes described in the preceding paragraph in virtue of the force exerted by two antagonist muscles. In vision the muscles of the two eyes stand to each other in what must needs be held as a very remarkable kind of sympathy or consent:—the opposite muscles in either eye always come into action together. This seems to depend on an association of the motions under the influence of the will, which by degrees becomes habitual. New-born infants cannot yet fix the axes of their eyes; the power is acquired by exercise; instinctively, however, for both eyes seem at once to follow the object so soon as the faculty of perceiving it is obtained. It is very possible by an effort of the will to bring the corresponding muscles into play; this in fact is necessarily done when we examine very minute objects closely; the eyes then converge, and this they do by the simultaneous action of the two internal straight muscles; we in fact then squint voluntarily inwards[708]. Morbid squinting is always a consequence of the preponderance of individual muscles of the eye; so that we have squinting in different directions; now converging, of one or of both eyes, and this is the most common kind; now diverging, which is much rarer[709].

§ 328. When the four straight muscles act together, the eye is drawn backwards in a right line into the orbit. Each muscle acting

excellent work of Ruete, *On Squinting*, already cited, where there is a thorough critical examination of the various views entertained in regard to the action of the muscles of the eye. I have followed Ruete principally, both in the foregoing and in the next succeeding paragraph. The action of the different muscles of the eye is a point that has acquired great importance lately, from the prevailing practice of dividing the muscles in cases of squint.

[708] We cannot, however, by any force of the will, cause the visual axes to diverge. Müller explains this from the congenital tendency to simultaneous motion of those muscles which receive corresponding or correlative branches from the oculo-motor nerve. The view of Ruete appears to be better founded, according to which, the impossibility of squinting outwards arises from a natural preponderance of the recti interni, which are the strongest muscles of the eyes, and are besides attached more anteriorly or nearer the cornea than the recti externi. The recti inferiores et superiores, which come into play when the pupil is rotated inwards, are also attached more anteriorly than the recti externi. This anatomical arrangement perhaps explains the greater comparative frequency of strabismus convergens. Both of the notions now quoted, however, are merely hypothetical, and much might be alleged against either.

[709] See Ruete, l. c. where the views of Müller, Valentin, &c., are criticised.

singly, turns the pupil towards itself. Two neighbouring muscles acting together, draw the pupil in a line, which is the diagonal of the two forces; the superior oblique acting by itself draws the posterior and superior part of the globe forwards and inwards, by which the pupil is made to describe the segment of a small circle directed downwardly and outwardly. The inferior oblique rolls the eye-ball downwards and inwards, and causes the pupil to describe another segment of the same small circle directed upwards and outwards. But if the two oblique muscles act together, then the eye is not turned on its axis, but is drawn forwards, or from the object, by which a force is engendered, which is directly opposed to that of the four straight muscles acting together. The eye-ball is at the same time slightly approximated to the inner wall of the orbit. It is easy to conceive how the several straight muscles may enter into combined actions with one or other of the oblique muscles. Should it be wished, for example, to direct the pupil very much upwards and outwards, the rectus externus is brought into play in combination with the obliquus superior, and the pupil is no longer moved in a small circle but in an ellipse, the diagonal of which lies in a direction betwixt the line of traction of the superior oblique and that of the external straight muscle. In case the pupil is turned downwards and outwards, the moving force is a compound of the action of the external straight, and the inferior oblique, muscles, and the diagonal of the ellipse in which the pupil then moves is intermediate between the lines of direct traction of these two muscles. When both eyes are tranquilly directed to an object at the proper distance for distinct vision, all the muscles act gently and harmoniously, and the pupils are directed straight forward, with a very slight inclination inwards, in consequence of the natural arrangement, so that the axes of the eyes, although nearly parallel, are not altogether so; greatly produced they would intersect at an extremely acute angle.

§ 329. If perfectly definite images are to be formed upon the retina, the crystalline lens, as the most important of the refracting media of the eye, must be at a determinate distance from the percipient surface. But the focal distance of the image is not the same for near and for distant objects. The focus of a near object is farther from the lens than that of a distant one. This is in virtue of

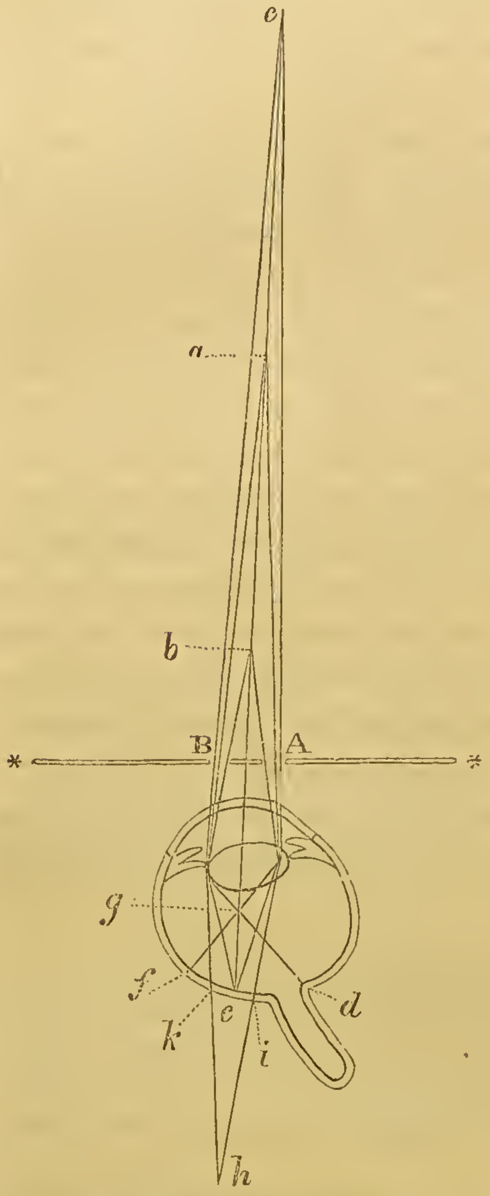
an indubitable optical law[710]. It is easy, however, to satisfy oneself by experiment, that changes must and do take place in the interior of the eye, when we look from an object that is nearer, to one that is more remote. We can in fact only see one of two objects, supposing them in a line and at unequal distances, with perfect distinctness at a time. If, for example, a small object, such as a pin, be stuck up at the distance of six or eight inches from the eye, a distance at which it can be seen with all conceivable distinctness, and some other more remote object be selected in the same line, so that both objects may fall precisely in the axes of the eyes; if one eye be now closed, and the near object, the pin, be steadily regarded, the distant one—the tree, the spot on the wall,—whatever it may be, becomes indistinct, it appears two-fold, it is shaded, it escapes from the sense of sight entirely; if the distant object be now steadily fixed by the eye, it immediately starts from obscurity into distinctness, and the pin becomes hazy and uncertain. We are even conscious when we direct our attention to the subject, of an alteration taking place in the eye, under these circumstances[711]. The faculty, however, which enables us to judge of distances, and to adjust the eye so as to obtain distinct vision at different distances, although it is probably only gradually acquired, is generally exerted unconsciously. The power of thus accommodating the eye is possessed in very different degrees by different individuals; it is particularly remarkable in some of the higher animals[712]; and in some men is either totally wanting or is reduced

[710] The tract of Olbers: *De internis oculi mutationibus*, Gotting. 1780, is interesting upon this point. Supposing the cornea and crystalline lens to maintain their several convexities unchanged, the lens must shift its position to the extent of about a line in order to answer for objects close at hand, and at infinite distances. According to Young, the needful change of position is equal to the sixth part of the axis of the eye.

[711] On this and other instances see the admirable Essay of Hueck: *On the motions of the crystalline lens—Die Bewegungen der Krystallinse* Dorpat, 1839.

[712] The power of accommodating the eye to perceive objects at different distances is very wonderful in birds of prey—vide Hueck, l. c. Hueck tells us that he had come to the conclusion from repeated observation, that the power of accommodating the eye to near and distant objects was possessed in highest perfection by country folks, day-labourers, carpenters, builders, messengers, gamekeepers, idlers, savage or half civilized communities, and by persons generally in the prime of life and vigour; on the contrary, that it was least perfect among soldiers,

to a minimum. Short-sightedness depends almost invariably on a loss of the power of accommodation in the eye, as a consequence generally of early and undue exercise of the organ upon objects close at hand. This defect is therefore almost entirely confined to persons in a certain rank of life, or having certain pursuits: the majority of scholars and men of letters are short-sighted. In the same way also far-sightedness is frequently an effect of the want of the power of accommodation in the eye: Sailors, who are always looking at the horizon, are all but invariably far-sighted. Both short-sightedness and far-sightedness are but the limits to innumerable and individual departures from that which may be held the standard in the structure of the eye.



§ 330. There are many experimental ways of proving the different positions which the images of near and distant objects occupy upon the retina. One of the best known is that of Scheiner[713], which has been variously modified by different observers. If in a card * *, two small holes be pricked, over or to the side of one another, but not more distant than the diameter of the pupil, A, B, and a small object such as a pin be looked at through them, it will be seen single only when it is at a certain distance from the eye,

sailors, coachmen, watchmakers, goldsmiths, copper-plate engravers, shoemakers, tailors, and the entire class of determined readers and writers. It is also gradually lost, as all the world knows, with the increase of years.

[713] Father Scheiner made this experiment more than 200 years ago: *Rosa ursina*, &c. 1626—29. Volkmann has suggested a great number of variations of the original experiment.

say at *a*; for the rays of the pencil which proceeds from the object at *a*, come precisely to a focus upon the retina, at *c*. If the pin be now placed at *b*, the rays will centre at *g*, in front of the retina, and the object be then seen double at *d* and *f*. The same thing happens when the pin is removed to a greater distance than *a*, say to *e*; the pencil of rays in this case could only centre after their refraction by the lens at *h*, far beyond the retina, so that the single object is necessarily again seen double at *i* and *k*[714]. Double vision of this kind sometimes occurs along with partial opacities, streaks and specks of the cornea[715].

§ 331. If it be easy to obtain conviction of the facts announced in the preceding paragraphs, it is just as difficult to specify the means by which the alteration in the position of the lens with reference to the retina is effected. The reason of the accommodating power has been sought for in the motions of the iris, in the lengthening and shortening of the axis of the lens by a faculty inherent in its structure, in an alteration in the convexity of the cornea effected by the action of the muscles of the eye, etc. These views have all been lately proved untenable[716]. The most probable cause of the power in question is a positive change of place of the lens, effected by the ciliary processes, by the action of which it is brought forward, and at the same time, possibly, slightly compressed laterally. The most weighty grounds for

[714] The accompanying diagram also enables us to understand wherefore when any object is too near to the eye, at *b*, for instance, and one of the holes in the card is closed, the double image immediately becomes single, that upon the opposite side disappearing: the ray *d*, is then intercepted, and of course its effect upon the retina is not produced. Again, if the object be at *e*, and the hole *B* is shut, the duplicate image disappears as before, but this time it is the image of the same side that vanishes.

[715] Ruete had lately occasion to observe such a case in a patient affected with leucoma, where the iris had coalesced inferiorly with the cornea, an opaque streak which took its departure from the leucoma, divided the pupil perpendicularly into two lateral halves. Objects at the distance of from 18 to 20 inches and more, appeared double. By the local use of calomel the streak was gradually removed, and single vision returned.

[716] Hueck and Ruete have both advocated a change of place of the lens by the action of the ciliary body as cause of the power of accommodation in the eye; Hueck in particular has gone to the bottom of the subject with great ability. Several older observers, however, had already espoused the same opinion.

assigning the accommodating power of the eye to motions of the lens are these: 1st, The concurring testimony of all, which is to the effect that the accommodating power is greatly diminished after perfectly successful operations for cataract; 2nd, The anatomical disposition and structure of the ciliary ligament, and of the ciliary processes, which are composed of involuntary—in birds even of transversely striated and voluntary—muscular fibres, which lie upon or over the edge of the capsule of the lens, are attached between the folds of the zonula, and, by contracting, must move the lens; 3rd, The sympathetic or consentient motions of the pupil along with the act of accommodation: the motions of the iris and this act are certainly associated in the relations of cause and effect, of effect and cause; for not only is the fibrous tissue of the external or posterior aspect of the iris in anatomical connexion with the anterior edges of the ciliary processes; but the functional implications of the one influence those of the other,—when a solution of belladona is dropped into the eye, for example, the pupil is enlarged, and the accommodating faculty is at the same time greatly diminished; an effect which certainly does not depend on the degree of contraction or of dilatation of the pupil[717]. 4th, Direct observation of the eyes of men and animals. The careful observations of more than one inquirer satisfy us that when, according to the laws of optics, the lens ought to advance, the iris is at the same time seen to become more convex, or to advance also[718]. The extent to which the muscles of the eye

717 That the pupil dilates when a distant object is viewed, and contracts when a nearer one is contemplated, is a fact. These motions are, however, consentaneous or concurrent motions only; either in consequence of the motion of the ciliary processes, or, as others will have it, from association with the motions of the muscles of the eye through the influence of the oculo-motory nerve upon the ciliary ganglion and the nerves of the iris. Contraction of the pupil always occurs along with contraction of the internal rectus, and of several other of the muscles supplied by the nerve just mentioned. [It would be interesting to ascertain whether or not, in the birds which have cross streaked and voluntary muscular fibres in the constitution of the ciliary processes, there were any filaments of nerves sent directly into the eye from the oculo-motor or another nerve, and without passing through the ciliary ganglion. R. W.]

718 Ruete and Hueck, make this statement, although for my own part I cannot be certain that it is correct. A person possessed of good power of accommodating his eye to near and distant objects, should be placed properly for observation, with one eye closed, and desired to look successively at a distant object, and at one close at hand—the head of a pin stuck within a foot of his eye. To

concur or aid in the act of accommodation is not yet satisfactorily settled[719].

§ 332. In ordinary vision the eye is a perfectly achromatic instrument;—we see objects with the colours they naturally possess, and with no others. The achromatism probably depends on the composition and combination of the refracting media, which, together, constitute the humours of the eye (§ 323). The eye is only achromatic, however, so long as the image is taken within the focus of the rays that form it. Bright coloured margins arise under certain circumstances; but they depend upon objective causes, and are not connected with chromatic aberrations produced by the lens or any other of the humours. The cause of the formation of dioptrical coloured borders is entirely different from that of the coloured images which arise from peculiar affections of the nervous substance[720]. Dioptrical coloured margins are always connected with refraction, and attach particularly to two conditions: (*a*,) a light must fall close to a shadow; and (*b*,) the limits of either must be projected on the retina in such a way that all sharpness of outline is lost. The transition from light to shade, the blending of the light and dark thus produced, then shows itself in rainbow tints. Those that appear most frequently are red, orange, yellow and blue, and occasionally beyond

see the arching the observer must look quite into the side of the eye. [Were the head of the person who is the subject of observation placed in a frame supporting a micrometer, as was done by Mr. Ramsden in his experiments, (*Philos. Trans.*, 1795,) the alterations in the position of the iris would become much more perceptible. R. W.]

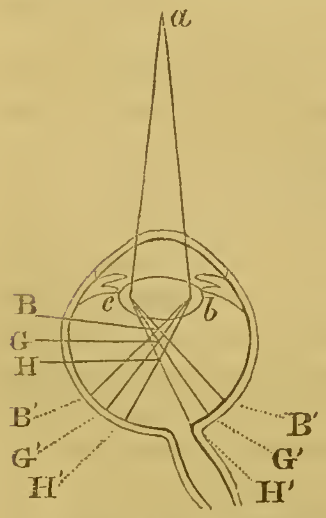
719 Although recent observers have spoken decidedly against the idea of the eye gaining its accommodating power through the action of its muscles, the following considerations appear to me to give it countenance: 1st, The muscles by acting together draw the globe of the eye backwards, and so shorten it, or forwards, and so lengthen it; 2nd, The feeling of weariness and almost of pain which I experience plainly in the circumference of the globe of the eye, and as it appears to me in the muscles, when I make efforts at accommodating my sight to objects not within the sphere of easy vision to me; 3rd, From the motions of the iris so constantly associating themselves with other muscular motions, that certainly depend on the oculo-motory nerve. At all events, it seems that further observations are still requisite before we decide that the muscles are altogether inoperative and inefficient in the faculty which the eye possesses of accommodating itself to near and distant objects.

720 On the coloured halos, the persistent images which follow experiments on dioptrical coloured margins, and which depend on an affection of the retina, see later, § 336.

the blue a faint violet. The phenomenon now mentioned is best produced by taking a position at the end of a room before a brightly illuminated window, and holding up any small object, such as a pencil, before the eye, which must be steadily fixed upon the window sash. By and by bright colours in the order just indicated will be seen to appear on either side of the bars as well as of the pencil. In the same way a clear field upon a dark ground, or a dark field upon a light ground, may be tried, and a biconcave or biconvex lens pushed before the eye. In either case the edge of the image appears surrounded by a coloured halo, in which, when the convex glass is used, red and yellow are the predominating colours; when the concave glass is employed, again, blue is the prevailing tint[721]. This is a very important experiment with reference to the theoretical portion of the doctrine of colours[722]. It may seem trivial to observe that it may be varied, and others like it in great numbers contrived. The coloured borders appear with unusual brilliancy when the lateral rays,—those that are usually intercepted and prevented from entering the eye, are admitted, as they may be by instilling a single drop of a saturated solution of extract of belladonna into

[721] On this point, consult the admirable essay of Tourtal: *Chromatics of the Eye—Die Chromasie des Auges* in Meckel's *Archiv*, 1830, S. 129, and Müller, *On the comparative Physiology of Vision—Zur vergleichenden Physiologie des Gesichtsinnes*, p. 194, et seq.

[722] The accompanying figure may illustrate this point. From the illuminating point *a*, a pencil or cone of light is emitted. The rays which fall upon



the edges of the lens *b c*, suffer decomposition into their constituent coloured rays, according to the laws of dioptrics. The most refrangible or blue rays cross the soonest at B; the least refrangible or red rays at the greatest distance from the lens, at H, between these two the yellow finds its place at G. No account is here taken of any save the three principal rays of the spectrum. Beyond the point of intersection, and where the images come to fall upon the retina, the colours must of course appear in reversed order (§ 324); and the eye, in fact, perceives them in the order B', G', H', blue, yellow, and red, instead of red, yellow, blue, which is their sequence in the spectrum. Vide Tourtal, l. c. p. 139.

[723] Numerous experiments are detailed in Goethe's *Farbenlehre*. Goethe explains all chromatic phenomena on the sole ground of modifications in the light and the dark—light and shade. In the light seen through dull media,

the eye with which we mean to experiment[724]. It is to be observed, however, that in having recourse to this means, the power which the eye possesses of accommodating itself to the perception of objects at different distances, is very much impaired, as already remarked (§ 331).

Actions of the Retina; Subjective Visual Phenomena.

§ 333. If the images of objects which are formed upon the retina are to excite in the mind perfectly definite perceptions, they must be produced at the proper focal distance from the lens, (§ 329,) and fall close to the point which corresponds to the axis of the eye, (§ 325,) within the limbus luteus (§ 319). Besides this, the objects must be duly lighted to excite the peculiar energy of the sentient parts of the retina; excessive illumination dazzles as much as defective light obscures. Farther, the objects must have a certain magnitude, in order to produce distinct images. There appear to be extremely minute particles in the retina, which are susceptible of receiving distinct impressions, or that enable us to perceive minute objects apart from one another as they are in nature. Beyond these minutest particles, the impressions mingle. We have a very excellent illustration of this truth, in the effects of copper-plate engravings. These, as is well known, are made up of dark lines or dots of different sizes, and placed at different distances upon a ground. Seen at a certain distance, these lines or dots blend into harmonious shades, and the general effect is produced; but inspected closely, each dark line or point meets the eye by itself, makes an isolated impression upon the retina, and is

when the dimming is moderate, we perceive yellow, then red, pale blue, blue, violet, black-blue, finally, black. If in the experiment detailed above, the lens which is held towards the image be gradually approximated to the eye, the bounding line fades, and it seems as if the dark encroached upon the side of the light, and the light upon that of the dark, with decreasing intensity as the boundary is passed. Goethe explains the dioptrically formed coloured margins from the subjective side, by a mutual encroachment of the light and dark, for the shadow before the light is perceived as blue and violet, and the light before the shadow as red and yellow.

[724] See Müller—*Physiology of Vision*, p. 199.

judged of simply as a line or point[725]. The distance at which objects can be perceived most distinctly, and in all their details, with the naked eye, is found in the generality of individuals at from eight to ten inches; this is spoken of as the point or distance of distinct vision. It varies in individuals according to their short or long-sightedness (§ 329); every eye, however, has its point of limitation for distinct vision. At this point, every part of the object attains the retina, at least every part the visual angle of which in the eye is of sufficient magnitude (§ 324). It is generally assumed that the smallest angle under which two points can be perceived as isolated, is of forty degrees, perhaps it is even less. From this it can be shown by calculation, that luminous rays from two points only blend, and occasion a single perception when they fall upon parts of the retina that are no more than $\frac{1}{600}$th of a line apart from one another. The percipient power of the retina is, therefore, at least 300 times greater than that of the tip of the tongue, which possesses the sense of touch in greater perfection than any part of the body; but where, as we have seen, the impressions of the two points of a pair of compasses at the distance of half a line, are still perceived as making but a single impression[726]. It is rather interesting to observe that the optical reckoning referred to coincides very nearly with the measurements of the minutest elements of the retina, the primitive fibrils and bacilli of which, as we have seen, have a diameter of from $\frac{1}{600}$th to $\frac{1}{800}$th of a line (§ 319)[727].

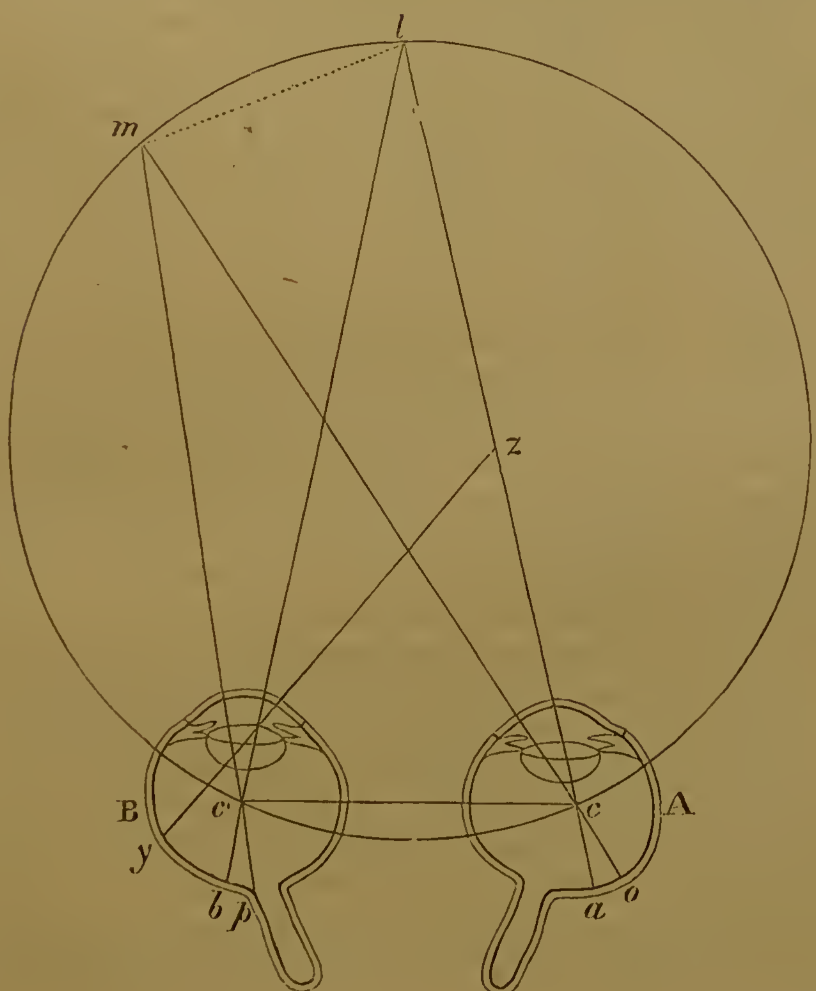
§ 334. Although there be two images formed by the refracting

[725] Microscopical objects show us what a variety of positively isolated colours combine to produce the impression made upon the unassisted eye. Many of the gray tints of nature, for instance those of the mouse's and mole's hair, are produced by the blending of the black and transparent elements of the objects. The green of many feathers, for example, that of the coal titmouse, of the mirror in the wing of the wild-duck, &c., results from a mixed impression of blue fields upon a yellow ground.

[726] Mueller (*Physiology*), Volkmann, (l. c. p. 201), and Weber (Mueller's *Archiv*, 1835, p. 159), have entered into the subject of these calculations.

[727] Volkmann thinks he is authorized to conclude from his observations, that the smallest retinal images are smaller than the finest elements of the retina itself; but in the present state of our knowledge touching the intimate structure of the retina, it would be premature to pronounce any definite judgment upon this point.

media upon the retina of the two eyes, still in ordinary vision we see objects single, not double. This depends on the condition or quality of particular spots of the two retinæ. Objects, to wit, are seen single when the axes of the two eyes meet in the object contemplated. In this case the point fixed by the eyes, *l*, in the accompanying diagram, falls upon the two terminal points of the two eyes' axes, *a* and *b*. The points in the two eyes, A and B, which correspond or are similarly situated, with reference to all surrounding points, are entitled IDENTICAL, inasmuch as they comport themselves subjectively as if they were in reality but a single point, and images impressed upon them excite in the mind the idea of but one image. Besides these there are other points of the retina which are also identical or correspondent; in other words, which present single mental conceptions of double retinal impressions; but it is a law that the objects and corresponding points of the retina must lie in a certain circle which is designated



the HOROPTER,—a circle which passes at once through the point of coincidence, *l*, of the visual axes, *l a*, *l b*, and the points of decussation *c*, *c'*, of these axes with the lines of direction. (Vide § 324.)[728] Objects which lie in the same horopter, such as the points *l* and *m*, will be seen singly, inasmuch as their images must necessarily affect corresponding points of the two retinæ. The axal points of both retinæ are therefore identical, and so are points, such as *o* and *b*, which lie at equal distances from these axes, and this, whether they be to the outside or to the inside of the axes respectively, or to the outside of the one, and the inside of the other: although *p* falls to the inside of *b* in B, and *o* to the outside of *a* in A, *m* is still seen as a single object. Objects or points that do not fall in the same horopter, on the contrary, cause the perception of double images, for they impinge upon points of the retina which have a different activity[729]. These points are consequently characterized as differential, and the two eyes now comport themselves as if different parts of the retina were affected in the same eye, a case in which, as we have already seen, two-fold images are formed, and are so perceived. (§ 332.) The axes of the two eyes, A and B, being fixed in the direction of *l*, the point *x*, (as also every point in the axis *a x l*,) will appear double; for its image falls in A, on the middle of the retina, *a*, but in B, it is projected at *y*, a point which bears no reference, or stands in no kind of relationship,

728 See Müller's *Comparative Physiology*, &c., p. 167, and Volkmann's *Contributions*, p. 86. Volkmann has given a very lucid exposition of these circumstances, which I shall here reiterate, referring always to the last diagram. Let *c c'*, be the two centres of the eyes A and B, *l*, the point regarded, *l c c'*, the horopter, *a* and *b*, the points of the retina on which the axes of the eyes terminate; and let *m*, be a second point in the horopter. The point *l*, appears upon the axal points *a* and *b*, the point *m* at *o* and *p*. A line betwixt *l m*, will form the cord of the arc of the horopter lying between *l* and *m*, and as all triangles drawn upon an arc of a circle have equal peripheral angles, so is the angle *l c m*, equal to the angle *l c' m*; both are farther equal to the opposite angles *o c a*, *p c' b*. Moreover, *o c*, is equal to *p c*, and *a c*, to *b c'*, as radii proceeding from the centres *c* and *c'* of the retinal circles, which in each eye have an equal circumference; consequently *o* is just as far from the axal point *a*, as *p* is from the axal point *b*, and so identical or corresponding points of the retina are effected by the rays proceeding from both *l* and *m*.

729 This is seen when in the course of the experiment just referred to, first one eye and then the other is shut for a moment, and the position of the objects is considered.

to *a*, in A. The double images then appear as far removed from each other, as the image, *a o*, of the right eye, A, appears removed from the identical point, *p b*, of the left eye, B. It is extremely easy to produce double images: we have but to hold up the fore finger of each hand, one pretty close to the eyes, the other as remote from them as possible, and then to look at either alternately; that which is fixed by the two eyes appears single, that which is not so fixed is seen double. From the laws of refraction already explained, (§ 324,) the position of the double images must necessarily be different. If the visual axes decussate betwixt the object and the eye, then will the left double image appear in the left, the right double image appear in the right eye. But if the visual axes first cross beyond the object, so that this lies between the eye and the point of decussation, then will the double image of the left eye appear to the right side, that of the right eye to the left side. We have necessarily many double images in our eyes at all times; but we do not attend to them by reason of their indistinctness. They become apparent the moment we attempt to fix two different objects at different distances in a line with each other. Double images also present themselves when the axes of the eyes are not kept parallel; if we chance to become drowsy over a page, the letters, and words, and lines that we read fly away from one another, and become double, and then as the attention is aroused they come together again, and appear single; the tipsy man also sees things double for the same reason; and so does he who squints, in consequence of one muscle of one eye being over-active.

§ 335. The congruity or disposition to be similarly affected in identical points of the retina, now considered, is innate, and has its efficient cause in the brain; so that the two eyes are to be regarded as so many off-sets from the same root. The grounds of the identity are therefore organic. This harmony of the two retinæ, this capacity to combine double impressions into one, is manifested everywhere in both eyes, a fact which appears especially from the phenomenon that has been spoken of under the title of the RIVALRY OF THE FIELDS OF VISION. If, for instance, a white surface, such as a sheet of paper, be regarded through two different coloured glasses held close to the eyes, the colours at first do not mingle; the paper does not appear green when a blue and a yellow glass are used, but it is either blue or yellow. By and by,

however, a change occurs; at one moment the yellow prevails, at another the blue; blue spots appear in the midst of a yellow field, or the contrary; and again, all is either blue or yellow, and so the thing goes on until one of the colours gains the ascendancy, and becomes permanent. In general the stronger eye,—and in many individuals one eye is much better than the other—prevails, and the field acquires the colour of the glass through which it looks; [although the thickness of the glass, and the relative depth of the tint of each have also their influence.]

§ 336. There is one very remarkable phenomenon which can be studied to great advantage in connexion with the functions of the eye, although it is general, and takes place in all the senses. This is the lingering influence of foregone impressions,—what have been called SPECTRA, with reference to the eye more especially. The subject of ocular spectra is one upon which many and most interesting experiments may be instituted to success, in the more delicate of which, however, a certain susceptibility of eye is necessary; for there is the greatest difference among individuals in point of retinal impressibility[730]. The stimulus of intense light, such as that of the sun regarded for an instant, leaves in the eyes of every one secondary images which only die off very slowly, passing through various shades of colour; feebly illuminated objects, again, whether coloured or colourless, leave no secondary image or spectrum behind them. Taking ourselves as the subject of observation, if we attempt to look at the sun, we are instantly forced to turn away blinded; the retina then shows us a perfectly black spectrum when we look upon a white surface, such as a cloud, or even the clear sky; but if the eyes be closed, or we look upon any dark surface, the spectrum is white. In the latter case, the spectrum passes through the series of colouring from bright to black: the white is followed by yellow, orange, red, green, violet, and finally, black, one after the other.

[730] Different eyes seem to have very different capacities to form spectral or after-images. Whilst I can excite them at any moment by looking at a copper-plate engraving with a white margin and a black frame, even in a very moderate light, I sometimes observe that one half of my auditors are unconscious of anything of the kind, even after inspecting brightly illuminated coloured quadrates. Want of attention and of the faculty of observation, however, seem frequently to be at the bottom of the circumstance now alluded to.

Was the image dark in the first instance, the series is the same, but reversed—upon the black comes the violet, green, red, etc. If we turn to the bright red of the setting sun or evening sky, the after-images go off from green to white; and contrast or complementary colours, as they are called, succeed the fixed inspection of differently coloured fields. The spectral or complementary colour of red is green, that of yellow is violet, that of blue is orange, and the reverse[731]. Black fields again appear white; white fields look black. These different impressions in the retina depend on the corresponding or stimulated part, subsiding from a state of high excitement into one of rest, which implies absence of all action, or obscurity. Spectral images are excited with the greater ease the more the eye has been tasked. Spectra always appear in the field of vision; that is to say, wherever or to whatever the eyes are turned,—to the floor, to the ceiling, to the right, to the left—there they are perceived.

§ 337. In the phenomena that have now been described, one appearance or impression upon the retina effaces another, and the secondary image only appears gradually, and after a lengthened impression of the primary image. There are other phenomena, however, where one impression so alters another, that the second remains along with the first, the second, however, being the opposite of the first. To this order belongs all exaltation or exaggeration of light and shadow, of coloured and colourless images by contrast. It is an admitted fact, that every shadow is exalted by

[731] It is easiest to study these complementary colours by cutting out squares or circles of brightly coloured glazed paper, and laying them upon a white ground in the sun or a very vivid light. The most striking experiments are those with red and green papers. To show the entire effect at once, however, a head may be painted in miniature with the face green, the coat scarlet, the hair white, and the waistcoat violet, the whole upon a black ground within a white margin. When the eye is turned from this picture to a white ground at the proper distance, the spectrum or after-image appears as a portrait, the size of life, with a ruddy countenance, black hair, green coat, and yellow waistcoat, upon a bright ground, the whole set in a black frame. The spectrum in this and other experiments of the same kind, only appears gradually, and after the white ground has been contemplated for a few seconds; it gains its maximum of intensity by degrees, and then begins slowly to fade. Goethe in his *Farbenlehre*, and Müller in his *Physiol. d. Gesichtsinnes*, indicate numerous multiplications and ways of varying such experiments.

contrast in the ratio of the intensity of the light by which it is cast, or as we say, by which it is viewed. One of the simplest experiments in connection with this point may be instituted every evening. For example, with two candles on the table, of the same illuminating power but some little way apart, let the shadow of a common pencil fall upon a sheet of white paper; two shadows are seen, of which that projected by the nearer light is always the deeper. If the more remote light be brighter than the nearer one, however, if a good lamp be substituted for the candle, things are immediately reversed; the shadow which is cast by the more distant but brighter light is now the stronger. Many coloured shadows depend on the same objective causes. Every shadow of a body cast by a coloured light is also coloured[732].

§ 338. In very many of the phenomena now mentioned, objective and subjective phenomena are blended or combined; for all modes or states of the senses depend on the mutual influence of external agencies and internal capacities or energies. It is on this account that contrast or complementary colours occasioned by objective colours (§ 336) often appear as subjective phenomena. A given colour requires a certain other colour to set it off, and these physiological or naturally pleasing contrasts of hues correspond with the complementary colours. For the same reason that deep shadows are produced by brilliant illumination (§ 337), do gray fields upon white grounds appear darker than when they are considered in themselves. From this it results that the retina possesses a certain genetic power:—under particular illumination, it considers colours, etc., in their simple states, and then, by virtue of a kind of reaction, it calls up contrasts which complete the original and simple impressions.

§ 339. These subjective considerations in the doctrine of colours lead us naturally to speak of the remarkable peculiarity presented by certain individuals, in reference to the want of power to distinguish one colour from another. It is well known that the judgment of many persons is singularly defective or perverted in

[752] On the topics discussed in the preceding paragraph, see the writings of Goethe and J. Mueller already quoted, and also the essay of Tourtal, *On the appearance of Shadow—Die Erscheinung des Schattens*, Berlin, 1830, in which there is much that is ingenious on the physiological circumstances connected with the production of shadows.

reference to certain hues. They cannot distinguish green from red, brown from blue, etc. This peculiarity in a restricted sense is more frequent than is commonly imagined. The generality of persons distinguish one bright colour from another; but very many have no perception, or only a very imperfect perception, of what are called shades of the same colour. It is remarkable that red, one of the very bright colours, and its complementary tint green, should be those in which the greatest and most general deficiency is experienced: red, and green, and gray, cannot be distinguished from one another. The power to distinguish yellow is very seldom affected; still many do not discriminate readily or accurately between this colour and pure white. The extent to which the refringent media of the eye, or perhaps the chromatic apparatus of the retina, (the columnar layer?) contributes to this peculiarity, is unknown. It is curious to remark, that the most frequent and striking deficiency in the perception of colours is in connection with the least refrangible ray, viz. the red[733].

[733] See on this subject the experiments of Seebeck, in Poggendorff's *Annalen*, B. 42. Among twenty persons there was always found one or more who had the faculty for colour imperfectly developed. Such remarkable instances as the following are rare: Goethe speaks of two individuals who could not distinguish rose-red, blue, and violet, nor green, deep-orange, and reddish-brown, from one another, so that a rose, to take a single example, appeared to them of precisely the same colour as the sky. Wardrop quotes the case of a man who could only distinguish yellow and blue, amidst the entire circle of colours, which all appeared to him mere modifications of these two tints. The shades of green were always referred by him to yellow or to blue, as either of these colours predominated in the mixture. Grass he called yellow of a deeper shade than gamboge, and very near to orange. Red and olive he regarded as identical, although, when he had the two together, he could occasionally distinguish between them. Cinnabar and bright reds he called yellow, carmine and its tints were blue; a scarlet coat for instance was yellow, a crimson scarf was blue; red-ink in the bottle was yellow, dried upon paper it was blue. The tract of Szoklaski: *On the perception of colours in a physiological and pathological point of View—Ueber die Empfindung der Farben*, &c., Giessen, 1842, contains many other instances of the same thing. [The function of the eye is most probably limited to the perception of light; any quality of an external object, other than the degree of its illumination, which we recognize through the medium of the eye, is connected with an internal faculty, with which that quality is in relation; the eye is no more the seat of the sense of colour, than it is the seat of the sense of configuration, number, or position. It is with the sense of colour precisely as with the sense of musical sounds: we may have as good eyes as any

§ 340. All the phenomena hitherto considered stand more or less in causal connection with the excitement of the eye, and particularly of the retina by brilliant light, considered as a physical quality of a peculiar kind. There are other phenomena of the retina which depend on its excitation by other powers, and these are particularly designated SUBJECTIVE VISUAL PHENOMENA. The laws of optics have no immediate influence on the knowledge of these phenomena; still it is highly interesting to contrast them with the condition of the retina produced by the stimulus of light. What is understood by stimulation or excitement of the retina by light, corresponds or is identical with the alterations in the dynamical state of this membrane which we experience in ordinary vision. Repose, non-excitement of the retina, is the cause of the idea in the mind of darkness,—without the eye we could have no sense of light; unless the eye be susceptible and excited we have none; the world of vision is to us non-existent. We can satisfy ourselves by a simple experiment, however, that without images of external objects we can still feel that we have a retina. The interesting phenomenon of the vascular image in the eye would satisfy us of this. The vascular image is most readily produced by holding or moving in a circle a bright taper or wax-light within a few inches of the eye. Gradually we acquire the impression of an ample bright field, which moves with and before the eye; this is the excited or illuminated retina. The field, however, is not uniform; dark arborescent ramifications make their appearance upon it, which have the exact anatomical characters of the arteria et vena centralis retinæ; we can even perceive the dark parts where the vessels pass through the optic nerve. This very interesting phenomenon, which in fact seems calculated to give us the best idea of the mode of action or affection of the retina, arises from the parts of the retina which are

in the world for perceiving objects, their relations, positions, magnitudes, &c. and yet be incapable of distinguishing red from green; just as we may have the quickest ears for the gentlest whispers, and yet perceive no difference between one note or one tune and another. There is an internal faculty which perceives light through the eye, another which perceives sound through the ear; if we have knowledge in addition of the qualities or peculiarities of light, which we designate colour, of the qualities or peculiarities of sound, which we designate tone, this is in consequence of the possession of two other internal faculties with which these new kinds of knowledge are in relation, and with nothing else. R. W.]

impinged upon and excited by the luminous rays appearing as self-illuminated fields, between those that are covered by the vessels, (§ 319,) and that are consequently not so powerfully excited by the rays of light as to retain any impression. It is in this way that the vessels become visible as dark ramifications upon a bright field[734].

§ 341. Other subjective optical phenomena may be produced by other stimuli in the most multifarious ways. 1st, We have pressure figures. By the pressure of the point of a finger or the head of a pin upon the eye-ball through the eye-lid we excite a variety of luminous figures—rings, crosses, stars, checquers, chains, etc., which are also produced by squeezing the eye-ball with the orbicularis palpebrarum muscle, or moving the eye suddenly and with an effort from one side to another. The situation in which these pressure-figures appear, is remarkable; they are always directly opposite to that pressed upon. If the part towards the inner angle of the eye be tried, a luminous ring is immediately seen towards the outer angle, and at the same time a bright spot at the point of pressure; by pressing on the lower part, the luminous ring appears above, by pressing above it is below, etc.[735]. 2nd, The galvanic or electrical stimulus causes luminous forms or flashes; the optic nerve is indeed the most susceptible of all the nerves to this stimulus. A single pair of plates suffices, in excitable individuals, to produce little flashes like those of lightning in the eyes; and with the galvanic pile, or the apparatus of induction previously mentioned,

[734] On the topic generally of subjective visual phenomena, see the admirable work of Purkinje, quoted in § 311. The experiment just described succeeds with the greater number of persons, not with all. [It strikes me that the phenomenon above referred to is no fair instance of subjective vision—*i. e.* of an action of the retina by which certain impressions are presented to the mind independently of external excitement. It is rather a secondary effect of a somewhat powerful antecedent local stimulation. It is obviously of the same nature as the singing in the ears that succeeds the subjection of these organs to the excitement of loud noises. The topic of subjective vision will be found farther discussed in the next paragraph. R. W.]

[735] These pressure-images are readily studied in our own persons at all times; Purkinje and Mueller, (l. cit.) have spoken of them at length. [They also occupied the attention of the late Mr. Fearn, a distinguished metaphysical writer, who published a work on the subject under the title of *Cerebral Vision*, with several appendices. R. W.]

(§ 243), large sheets of light present themselves to the vision, on establishing and breaking the circle, even when the poles are applied to distant parts of the body[736]. 3rd, Luminous and phantastical forms, indeterminate and determinate, waves and sparks, images of objects unknown and known, faces beautiful and hideous, landscapes often beautifully tinted, etc., appear to us in the depth of the night, and with closed eyes, particularly as we are dropping off to sleep, and in the course of our dreams. The impressions we receive in this way are often so strong, that even on becoming wide awake we have difficulty in persuading ourselves that all has been unreal, that we have been the sport of our own partially active senses and internal faculties. Many of the phantasms perceived under such circumstances are recognised as after-images, as renewals or repetitions by the senses of previously received impressions, at the dictates of the compound mental act which we call the imagination[737]. 4th, Pathological phantastical images, precisely similar to

736 I find the apparatus of induction very available here. If the poles be made to touch the internal surface of either cheek, the masses of light that appear are of extraordinary breadth; placed in the ears, girdle-like streaks of light pass round before the eyes. I have known the galvanic stimulus excite such luminous appearances in a case of almost complete amaurosis. Purkinje by using high powers produced more determinate and also coloured figures. With twenty pairs of plates the flashes were of a bright violet, and this by changing the pole, was changed into yellow. When he pressed any point of his eye at the time of the experiment, the galvanic luminousness appeared confined by the pressure-image, and by continued and augmented pressure, the arborescent figure of the eye described at § 340 was produced; every time a discharge took place the whole retina was illuminated with a most beautiful bright violet tint, which flashed from the point where the optic nerve enters, over the whole of the retina, of which a much larger portion became perceptible to the right and left than in the experiment as ordinarily performed with a taper.

737 This matter will be taken up again in the general physiology. When these subjective spectral images are vivid and permanent, and show themselves to the open eyes, they are always connected with a pathological cause; and they sometimes give rise to hallucinations. [This is one of the most interesting topics in the whole physiology of the senses, and it is one that is also highly important in a psychological point of view. It is in fact connected with dreams and visions, ghosts and apparitions, to which all men in the earlier ages of the world, and the ignorant, the weak, and the vulgar, at the present day, still attach so much importance. These are all as much subjective, or dependent on internal motions, as the circulation of the blood or the digestion of the food, and are no more connected with the prospects of individuals, or the current of events.

the physiological ones, are constantly occurring in the course of diseases: the fevered man's bed is surrounded by crowds of discordant and harmonious images; the patient affected with what is called delirium tremens, and the maniac, are attended in the same way, so also is he who is under the influence of narcotics, or who has merely some local mischief going on within his eyes. The appearances in the latter case are often distinctly referable to unusual action

than is the faint echo of the melody which we heard yesterday, and which haunts us through the whole of to-day. When the individual is aware that the spectre or apparition which has appeared to him, or that attends him,—for many men have had their familiar spirits to wait upon them continually for years, and that not always clothed in the most questionable or likely shape,—exists in his retina or in his mind only, that it has no existence in fact, he is labouring under a kind of insanity either of the retina or of that part of the brain which perceives visible objects. His proper consciousness and his reasoning powers are unaffected; he knows that beyond himself there is no such thing as that which he beholds. Sometimes we can assign a very satisfactory reason for the appearance of apparitions: we find it almost natural that to the mind of Brutus, meditating in silence and solitude on his past fortunes and the chances of the struggle in which he is then engaged, reverting at the same time with infinite bitterness to the first guilty step in his career, the likeness of the principal actor in the tragedy should take shape and substance before him. The ghosts that females and persons of affectionate nature have seen, are almost always the simulacra of dear departed friends,—mothers, sisters, lovers, &c. How grandly has our Shakspeare availed himself of this, as of all else that is natural in our constitution, when he marshals his hero with a phantom-dagger "the way that he was going," and before his very fixed gaze makes "gouts of blood to stand upon its blade and dudgeon, which was not so before." In this brief scene, the poet gives in fact the history of all apparitions: they are false creations proceeding from the "heat-oppressed brain," which, powerfully excited, "makes the eyes fools of the other senses,"—of the better senses, it may be, as well as of the worse. Dr. Ferrier and Dr. Hibbert, in their several works "*On Apparitions*," have treated this interesting subject in a more perfectly philosophical and enlightened spirit than any other writers. R. W.] The dreams of those who have lost their sight give us strong assurance that all such phenomena are but after-images. Shortly after their loss of sight, the blind have vivid dreams of coloured objects; but these dreams become gradually rarer and rarer. Even in cases where the retina and eye have been entirely destroyed, such dreams occur, and sparkles and flashes of light are occasionally beheld, before the eyes, as it seems, but in fact before or in that part of the brain which is the origin of the optic nerve and the immediate seat of vision. The poor patient is sometimes deceived by this, and believes that he has recovered his sight. Vide Hermann, *On Optical Delusions*, *Bildung der Gesichtsvorstellungen*, p. 165.

locally; there is a kind of turmoil and moving to and fro of luminous or dark points, which have often a pulsative motion. These very certainly depend on a consciousness of the motion of the blood in the vessels passing athwart the field of vision[738], in consequence of excitement and congestion of the circulating system of the eye. Perhaps the images that follow the administration of narcotics—opium, digitalis, belladonna, etc., are also explicable through the affection of the circulation that occurs under their use.

§ 342. If it be true that the operations of the soul have an immense influence over the actions of the organs of sense in general, it is especially so with reference to that of vision. We are in fact much accustomed to regard certain effects as immediate products of the action of the organs of sense, which are far rather connected with a higher act of the soul. This reciprocal influence is conspicuous in all the visual acts which we perform with purpose or intent. When we turn our attention to an object that attracts us, we perceive the most minute details that would else escape us altogether. We then go over the surface of the object with the axes of the eyes in the most favourable position for distinct vision, and our mind is wide awake to every impression that is made upon the retina; just as in feeling an object we pass our hand over it in all directions, and bring the largest possible quantity of surface into contact with it (§ 278). When, on the contrary, we are sunk in thought, when our minds are occupied with something else, we are apt to see nothing of all that lies or happens around us,—we stare vacantly from us.

[738] Steinbuch and Purkinje will have it, that they had seen the circulation in their own eyes. After great straining of the eye upon a bright white surface very close to it, Purkinje observed a clear circle to arise, and beside it a dark spot in the middle of the field of vision; here he observed two perpendicularly disposed faint lines, along which rows of blood-discs ascended in the one, descended in the other. By stooping for a moment, suddenly, it is very common to have the sense of sparks and flashes, owing apparently to the temporary congestion that is induced. In trying the effects of digitalis in large doses, on himself, Purkinje had luminous figures, concentric circles with rosettes in the middle, which he calls glimmer-roses, &c., present to his sense of sight, *loc. cit.* p. 120, Fig. 38—40. Purkinje concludes from his numerous and varied experiments, that behind the whole host of impressions of light, of indefinite shapes, &c., there is always something special and that with due attention can be referred to a definite form and quality—to impressions recently made on the retina, or strongly fixed in the memory, etc.

In judging of the distance of objects, we take into account their known magnitude, and the distinctness with which their several parts are seen; we at the same time call in our powers of comparison; we, in short, make use of our senses in conjunction with our other faculties, and then form estimates which through habit often appear to us as effects proceeding immediately from impressions made upon the senses, but which are, in fact, results of previous knowledge and experience, though they are not generally considered as such. Children, and persons who have gained their sight somewhat late in life after successful operations for cataract, have been said to see all things at equal distances, or on the same plane. Our judgment of the forms of objects by means of the eye is also acquired, or is the effect of experience. With all our experience we are nevertheless often deceived in the end, for we cannot see objects in a well painted picture otherwise than at different distances and possessed of substance, whilst they are all as we know upon a plane, and mere shadows[739]. Attention and exercise have im-

[[739] Metaphysicians and physiologists have puzzled themselves greatly about the capacity of the senses severally, to perform their own offices, and also in regard to the degree in which man and animals are what they are, through the operations of their senses. According to one school of philosophy, all our faculties, both intellectual and moral, and all our knowledge, are the effects of impressions made on the senses; according to another, the senses are the mere implements by which the mind works, and instead of informing the spirit, they are much rather perpetually leading it astray. These philosophers are, therefore, loud in their warnings against the illusions of the senses. A third school reject the senses entirely, and retiring into their closets propose to discover the faculties of the mind and their mode of operation, by meditating on the subjects of their own consciousness.—As simple physiologists, we must admit both internal and external faculties or senses, each of which acts by the medium of a distinct organ, which in every case suffices for its own function. All that has been written upon the mutual rectification of the senses, whether by one another, or by the internal faculties, must be received with much caution. I do not believe for instance that the faculty of judging of the relative distances of objects, is any effect of the internal intellectual act of comparison. The laws of perspective and the laws of vision are in harmony, and we must needs see this object nearer, that more remote, as we must see this to the right hand, that to the left, independently of all experience or previous knowledge. It is neither more nor less than a physical impossibility, that persons who have recovered their sight after operations for cataract, should see all objects on the same plane. They may not be able to judge of the precise amount of greater proximity or distance between one object and another, but if they see at all, they must see objects

mense influence in connection with the performance of its office by the eye. Nomadic races of men, inhabiting extensive plains and steppes, who are at the same time warlike in their habits, possess a keenness of vision of which we can hardly form any conception[740]. The language of the eye—THE LOOK, belongs to what we call expression, and is connected with the actions of the internal and external muscles of the eye.

§ 343. There is a great variety of other topics with which physiologists have frequently taken an infinity of pains to little purpose, most of the points being absolutely beyond the true province of physiology, and this science furnishing no data in regard to their explanation. To this division I would refer the enquiry: wherefore with reversed images upon the retina, objects are still seen erect? (§ 324). At the present time, that view according to which conceptions of reversed and erect, of right and left, are merely relative, is very generally admitted. Since the eye that regards, leaves all things in their local relations,—as it reverses all things, the soul or percipient principle has no term of contrary comparison; to see things in general, otherwise than reversed, one at least among them must show itself not reversed, and this is a contingency that can never happen. All attempts to explain the phenomenon of erect vision, whilst we have the retinal images reversed, must necessarily fail[741].

some closer at hand, others more remote. Neither do I believe that our ideas of form are effects of experience. Through what medium is the experience gained? Unquestionably the rays of light proceeding from a cube, impress the retina differently from those proceeding from a sphere, and engender the idea of a different image in the mind, in connection with the presence of each of these solids, and this at once and independently of all experience. In short, each sense suffices for its own function, and is independent of the other senses, and of the internal faculties. The eye perceives and judges of light and its degrees apart from every consideration of form, colour, number, &c. Every sense may nevertheless be greatly improved and strengthened by exercise, both by itself and in conjunction with the other senses and faculties. R. W.]

740 Recent travellers speak of the wonderful power of vision possessed by the inhabitants of the Asiatic steppes, who from clouds of dust upon the verge of the horizon, invisible to all other eyes, even when aided with the telescope, save their own, often proclaim the movements of enemies.

741 Volkmann and Müller have gone at length into this subject, and shown the deficiencies and errors of all the explanations. The literature on erect vision is very copious. Bartels' *Contributions to the Physiology of Vision*, Berl. 1834,

§ 344. As by means of the ear we recognise certain relations in tones, which form the basis of melody and harmony in music, so by the eye are we conscious of something of the same kind in reference to colours. Combinations of the complementary colours are always felt as agreeable to the eye, whilst associations of tints that stand in no kind of relationship to one another, make an unpleasant impression on the sight, and are held as outraging good taste. There is certainly a harmony of colours, as well as one of tones; and as all are not alike awake to the sequence of tones, and to the effects of combinations between them, so neither are all alike sensitive to tasteful combinations of colours, and this without any reference to the general excellence of the sight for ordinary objects. Savage tribes and the vulgar generally, are fond of glaring colours, red and yellow in particular, and they combine them without any offence to their eyes, never feeling the necessity of resolving the discord between them, by the introduction of a complementary tint. These are subjects in the study of the functions of the senses, that evidently interest art and its progress, more than the special physiology of man; they cannot, in short, be treated of isolatedly with propriety here; what else may fairly be said of them, belongs to the general physiology.

SECTION III.

OF THE STRUCTURE AND FUNCTIONS OF THE BRAIN AND SPINAL CHORD.

General Morphology of the Brain.

§ 345. We can scarcely be said yet to possess a philosophical anatomy of the brain. The mode in which the organ had hitherto been studied led to little more than the enumeration of certain particular and isolated parts, the forms and connections of which were sought to be learned by means of perpendicular and horizontal

and Berthold, *On the erect position of visible Objects*, Götting, 1835 (both in German); may be consulted on the subject.

cuts through its entire mass. This was merely a mechanical anatomy of the brain; and we in fact learned no more from it, than we should have discovered of the structure of the liver by slicing it first perpendicularly and then horizontally, and carefully describing the various appearances which we saw upon the surface of our cuts. Happily comparative anatomy and the history of animal evolution have lately given us some leading principles, and we may now hope for an assured and onward progress in this important department. It is interesting to remark that wherever an insight into the nature of the function or functions performed by an organ has been wanting, there has the structure also remained more or less obscure; we feel the want of everything like a guiding principle in the anatomical enquiry; of this truth we have satisfactory assurance in the cases of the thyroid, thymus, and supra-renal bodies and spleen. The functions of the parts of the brain are unknown to us, it is true, but then a general survey of the morphology of the organ, in which the object to be steadily kept in view would be to make out the essential, typical parts in its structure, might be expected to throw some feeble light upon the nature and connection of its elements.

In entering upon this task, we have as it were a fourfold path to tread. 1st, We have to investigate the various forms presented by the several parts of the brain in the animal series, and endeavour from this grand comparative survey to distinguish general or even universal conditions from such as are partial only or even accidental[742].

[742] The great importance of this mode of proceeding is now generally recognized. Müller, in his *Physiology*, says: "In no department of physiology can greater advantage be taken of comparative anatomical inquiries, than in that which has the brain for its object." B. ii. S. 805. This consideration has in fact led me to give a pretty extensive series of figures, illustrative of the morphology of the brain, in my *Icones Physiologicæ;* some few errors and omissions in which I have taken the opportunity to correct and supply in my *Icones Zootomicæ*, Lips. 1841.—The works of Tiedemann, on the brain, are classical.—*Icones cerebri simiarum et quorundam mammalium rariorum*, fol. Heidelb, 1821; *Comparison of the brain of the Negro with that of the European*, *Zeitschrift für Physiologie*, B. ii. and 4to, Heidelb, 1837. The figures of both Serres and Desmoulins are to be viewed as extremely imperfect: Serres, *Anatomie du Cerveau dans les quatre classes d'animaux*, &c., 2 Tom. 8vo, Atlas in 4to, Paris, 1827; Desmoulins, *Anat. Comparie du Systeme Nerveux*, &c., 2 Tom, 1825. We find much better figures of the brains of mammals in the work of Leuret: *Anatomie comparée du Systeme Nerveux dans ses rapports avec l'intelligence*, Paris, 1839, of which the 1st vol. and two numbers of the Atlas have appeared. At the

2nd, With these permanent forms thus discovered, we have to compare the brain in its different stages of development, in the fœtus and at various periods of life[743]. 3rd, We have to pursue the primitive fibres and their extensions from the nerves and spinal chord, and trace them as far as possible into the substance of the brain, to observe their relations to the aggregations of gray matter (ganglionic corpuscles) and their combinations one with another, as well as with the several divisions and subdivisions of the cerebral parts[744]. 4th, We have to question pathological appearances and phenomena, particularly congenital deficiencies and malformations of the brain, and to see whether from these aught can be won for the illustration of the functional phenomena of the healthy and well formed organ[745]. The association of these various lines of inquiry will by and by be found to supply us with certain general data for more particular physiological inferences.—It is presumed, of course, in entering upon this subject, that the reader is familiar with the details usually contained in elementary anatomical works[746].

present time, almost all our zootomical knowledge of the brain is confined to that of the arrangement and relative size of its larger divisions.

743 The history of the evolution of the brain has already been treated of fully in the First Book, to which I therefore refer.

744 Upon the carrying out of this principle, depends that satisfactory anatomy, and perhaps physiology, of the nervous system, which is yet in the womb of time. One of the greatest achievements in Anatomy would, in fact, be to give a graphic exposition of the fibrillation of the brain and spinal chord, even of a single animal—to resolve these parts in the frog, for instance, into their primitive fibres. At present there is no prospect for us in this direction; insuperable difficulties seem even to oppose the successful accomplishment of such a task. All we have hitherto had, has been a rude indication of the course of the principal fibrous bundles in the brain.

745 The pathological data we possess are both very few and very unsatisfactory. The defective knowledge among the majority of medical practitioners of the anatomy of the brain, the clumsy and incomplete dissections that are made of it, &c., satisfy us that we can only use the information obtained from such sources with the greatest circumspection in our physiological studies. Burdach, in his great work, *On the Brain*, has attempted to give a summary of the results obtained from post mortem dissections, and has shown, that no kind of general inference can be safely drawn from them. The older and more recent researches upon congenital idiotcy, and the cranioscopical inquiries, of which we shall speak by and by, are of far more importance.

746 The anatomical labours of the last century are as good as useless; even the extensive and careful work of Vicq D'Azyr: *Traité d'Anatomie et de Physiologie*, fol., Paris, 1786—90, is altogether unsatisfactory. Our better knowledge of the brain may be said to begin with Söemmerring, who nevertheless

§ 346. It is easy to trace a progressive advancement in the structure of the brain through the entire series of vertebrate animals from the fish up to man. In FISHES the several parts lie distinct from one another in the form of globular masses one behind another. If these divisions be followed in any of our commoner fishes, such as the pike, the skate, or dogfish, from behind forwards, we see the spinal chord, which is divided into posterior and anterior tracts or strands, precisely as in man, enlarging into the first distinct cerebral part—the medulla oblongata, which must needs be regarded as a true and integral portion of the brain. From this part arises the acoustic nerve—it is the cerebral part in immediate relationship with the nerve of hearing; but it does not exist for this alone; it is in communication with the whole of the other cerebral pairs except the two most anterior. The medulla oblongata is best and most properly entitled the POST-CEREBRUM. In front of the medulla oblongata, and also of the cerebellum, which will immediately be mentioned, we observe a pair of ganglions which in the bony fishes present themselves as a couple of large vaulted hemispheres, in the cartilaginous fishes again, as two much smaller hemispherical elevations. In bony fishes,

confined himself to the relative development of its several grand divisions, and to the origin of the nerves. His chief works are his *Tabula baseos Encephali*, 1799; *Academicæ adnotationes de cerebri administrationibus anatomicis*, in the Memoirs of the Academy of Munich, 1808, and his *Quatuor hominis adulti encephalum describentes Tabulæ*; edited by D'Alton, 1839. Gall is the next who deserves mention in connection with the anatomy of the brain, and his merits are great; his discoveries are consigned in the work of which he began the publication conjointly with Spurzheim: *Anatomie et Physiologie du Système Nerveux en général et du cerveau en particulier*, Paris, 1809—1819, 4 vols., 4to; Reil, however, had already begun the publication of his papers, *On the Anatomy of the Brain*, which he continued through the 8th, 9th, and 11th vols. of his *Archives for Physiology* (1807,-8,-9, &c.); and it must be allowed that Reil's plates are still among the best we possess, particularly on the structure of the cerebellum. [See what I have said before on the historical question here involved. R. W.] Burdach made a farther step in the right direction in his great work *On the Structure and Vital Endowments of the Brain,—Vom Baue und Leben des Gehirns*, 3 vols. 4to, 1819—26, which unfortunately is illustrated with too few plates. The best iconographic works on the brain of the present day are those of Langenbeck in his *Tabulæ Anatomicæ*, and especially of Arnold, in his *Tabulæ*, in studying which, the work of the same author, entitled, *Observations on the Structure of the Brain and Spinal Marrow—Bemerkungen*, &c., 8vo. Zürich, 1838, ought to be consulted. See also my *Icones Physiologicæ*, Tab. xxvii, where many of the most important points are brought together.

the pike for example, these ganglia are hollow internally, (they enclose the third ventricle,) and upon their floor several smaller ganglia, analogues of the corpora quadrigemina and corpora striata in quadrupeds and man, are developed; and more than this, certain transverse bands of connection, analogues of the posterior and soft commissures in the human subject. These middle parts or ganglia, from which the optic nerves take their rise by several large roots, I call the MESO-CEREBRUM. In cartilaginous fishes this division is narrower and smaller; it falls into a subordinate ganglionic pair, which represent the corpora quadrigemina, and a more anterior narrow part with a patent internal cavity (the third ventricle). From the meso-cerebrum the optic nerve arises in cartilaginous as well as in bony fishes. It is therefore the cerebral part in most intimate connexion with the optic nerve. Occasionally we observe accessory ganglia developed in its circumference.

Still farther forward, we come to another pair of parts or ganglia, which, in the bony fishes, are very small, lie much apart, and are connected by a commissure corresponding to the anterior commissure of higher animals. With this division we find the olfactory nerve connected, but not immediately, for the nerve seems rather to proceed from an enlargement situated in front of it, the olfactory ganglion. In cartilaginous fishes, where the olfactory nerve is larger than in bony ones, this division also presents itself more highly developed. I entitle it the PRO-CEREBRUM.

We have yet to discover the part which corresponds with the CEREBELLUM. We meet with it as an azygous enlargement in the cyclostomes, as a narrow commissure or bridge in the proper cartilaginous fishes, and as a much larger and often lobulated mass in the true bony fishes. Internally it contains a cavity which corresponds to the fourth ventricle in man.

The third ventricle is very commonly seen lengthened out into an infundibulum, connected with the extremity of which there is often a very large pituitary gland (hypophysis cerebri). It is doubtful whether or not fishes have any pineal gland; something analogous to it however exists both in the bony and cartilaginous orders, and even the cyclostomes have an azygous lappet which may be held its analogue[751].

[751] It therefore appears from the preceding view that there are three principal divisions recognizable in the brain of fishes, besides the indubitable cerebellum—

§ 347. We find the same essential forms of parts and mode of composition in the brains of AMPHIBIA which we have just noticed in fishes. The naked amphibia, such as the frog, newt, etc. approach most nearly to the lowest of the cartilaginous fishes in the structure of their brain. In front of the medulla oblongata we observe the cerebellum in the guise of a narrow medullary band, in which the roof of the third ventricle, as in the vermiform process of man, is continued. Before the cerebellum lie the corpora quadrigemina; still more anteriorly, and over the third ventricle, which extends further forward still, lies the pineal gland. In this way is the meso-cerebrum circumscribed, from which inferiorly the infundibulum and optic nerves are sent off. Still proceeding forwards we come to the two hemispheres, which, attached to the pro-cerebrum, take on a higher development; anteriorly from the pro-cerebrum the olfactory nerves arise.

In the scaly amphibia, the medulla oblongata, cerebellum, corpora quadrigemina, pineal body and infundibulum, all preserve the same relations; but the hemispheres are here notably developed, and the olfactory nerves take their departure from their fore parts. The hemispheres in the form of rolled laminæ, now form the side walls of the lateral ventricles, and close in their cavities more completely than we have yet observed them to do. Upon the floor of the lateral ventricle we perceive certain ganglia—corpora striata and nucleus lentiformis, and the choroid plexus.

§ 348. BIRDS present a very uniform arrangement of the cerebral parts. The medulla oblongata or post-cerebrum, is considerable; a proper pons is still wanting, but a few transverse medullary streaks stand in its stead. The cerebellum bears a great analogy to the vermiform process of quadrupeds largely developed, the

these are the post-cerebrum, the meso-cerebrum, and the pro-cerebrum, which are in direct connection with the organs of hearing, sight, and smell. The pro-cerebrum I regard as the analogue of the cerebrum of man and the higher vertebrata; but it is still extremely rudimentary. This is not the place to enter into the controversy which has arisen among zootomists in regard to the meso-cerebrum of bony fishes—vide my *Elements of Comparative Anatomy*, § 279, and Müller's *Physiology*. In studying the anatomy of fishes, from the Myxine glutinosa upwards, we see very beautifully how the brain is gradually evolved throughout the series upon the fore end of the spinal chord.

hemispheres or lateral parts being merely indicated; it is divided into laminæ by transverse fissures. One portion of the medullary strands of the post-cerebrum expands in its interior, and gives off branches that are covered with gray ganglionic masses, and so form an arbor vitæ. Transverse medullary bands (commissures) come into view when the corpora quadrigemina, which are of considerable relative size and are developed outwardly and inferiorly, are pushed aside. More anteriorly we meet with the third ventricle, bounded in front by the anterior commissure, which can be traced expanding on either side into the cerebral hemispheres, which are masses of considerable size, and from the anterior inferior parts of which the olfactory nerves with their usual bulbous enlargements take their rise. Pineal and pituitary bodies are distinct. The hemispheres are still smooth, without convolutions and without posterior lobes, so that the cerebellum altogether uncovered by the cerebrum lies immediately behind this. There is no more than a mere rudiment of the corpus callosum, the great commissure of the hemispheres, present.

§ 349. Among MAMMALIA, the monotremata and marsupiata have the least perfect brains. In the latter, the hemispheres, particularly behind, are but little developed, and the corpus callosum is still rudimentary, as in birds[752]. In the ornithorynchus the cerebellum greatly resembles the same part in birds, being developed almost exclusively in its vermiform process, and the cerebral hemispheres become very narrow and pointed as they advance. The pons or commissure of the cerebellum, however, appears to be general. In the lowest orders of the class,—the rodentia, edentata, and marsupiata,—in the whole of which the cerebral hemispheres are smooth, unmarked by convolutions, and imperfectly developed, not only does the cerebellum lie free and uncovered, but the corpora quadrigemina and pineal gland do the same, so that they come into view at once[753]. The vermiform portion of the cerebellum is still much more highly developed than the lateral

[752] According to Owen's interesting inquiries in *Philos. Trans.* 1837, p. 1, the corpus-callosum appears to be wanting in the greater number of marsupians; it is here no more, in fact, than a small band which connects the hemispheres.

[753] See the figures of the brains of the ant-eater, and migratory rat, in *Icon. Zootom.*, Tab. viii, Fig. x. xi.

portions. In some of the smaller monkeys of America, the cerebral hemispheres are still quite smooth, but their posterior lobes are so well developed, that they cover the cerebellum for the major part. In the feræ, convolutions are always present, and so are they in the ruminantia; in the rounded brain of the porpoise, they are remarkably well developed and very numerous; the posterior lobes, however, are but imperfectly evolved, and leave the cerebellum partly uncovered[754]. The corpora quadrigemina are frequently hollow within, and relatively larger in the lower than in the higher orders; the thalami optici, on the contrary, increase in relative size, as we ascend in the order. The corpora striata appear to be relatively larger in the more inferior orders. Corpus-callosum, fornix, and septum-lucidum, are all present, although they are but imperfectly developed in the lowest orders. The corpora albicantia in general form but a simple prominence. The lateral-ventricles are of small extent about the middle, and particularly posteriorly. The cornua Ammonis are generally very considerable; but, on the other hand, the pedes-hippocampi and the posterior cornua of the ventricles are absent. In by far the greater number of mammiferous animals—rodents, ruminants, pachyderms, marsupians, edentata, and carnivora,—the immense enlargements by which the olfactory nerves take their rise, are a remarkable feature. They are always hollow, their cavities being in immediate and free communication with those composing the lateral ventricles, and they present themselves as lobules of considerable size, under and in front of the proper cerebral lobes[755].

§ 350. The comparison of the human brain with that of the ouran and chimpansee, as the two creatures that approach man most closely in their general organization, and those of the dog and elephant, as the animals that in intellectual constitution are acknowledged to stand at the head of the animal series, is a subject of peculiar interest[756]. It is well to preface this matter, by taking

[754] See the brain of the giraffe and dolphin, in *Icon. Zootom.*, Tab. viii, Fig. 6, 7, 9.

[755] Farther details in my *Elements of Comparative Anatomy.*

[756] See the series of figures illustrating the cerebral configuration of the mammalia, contrasted with the brain of the female Bushman, in *Icones Zootomicæ*, Tab. viii.

a survey of the brain of the monkey—Cercopitheeus—that may be regarded as typical of the order. Here, the brain evidently resembles that of man, in configuration; the hemispheres are well developed posteriorly as well as anteriorly, and only leave the cerebellum uncovered in the middle. The convolutions, however, are few in number, but perfectly symmetrical, the same furrows and ridges presenting themselves on either side[757]. The cerebellum is of very large relative size, the lateral lobes are much developed. The medulla-oblongata is of great magnitude relatively to the brain; it presents the same parts or eminences—pyramidal bodies, olivary bodies, etc., as in man. Behind the pons, which is of good dimensions, we perceive a transverse fasciculus, the trapezium, which is wanting in man. The corpora albicantia form a single projection behind the infundibulum; the corpora quadrigemina, particularly the more anterior pair, are of very great size; the olfactory nerve is without any mammillary process, and more like that of man. The posterior cornu of the lateral ventricle and the pes hippocampi are wanting. The brain of the ouran, and particularly that of the chimpansee, bear a closer resemblance to that of man[758]. The hemispheres are here more largely evolved, the convolutions more numerous, not quite symmetrical, but still bearing a certain analogy on either side; the cerebellum is much larger relatively to the brain than in man, but the trapezium is wanting here, as it is in the higher being; the corpora albicantia are now distinct; the posterior cornu makes its appearance, and on the cornua Ammonis we perceive those impressions, which are designated pes hippocampi, and which, with this solitary exception, only occur in the human subject.

In the dog the development of the hemispheres falls off along with that of the convolutions; the corpora albicantia are, however, still double here. The elephant appears to have the most numerous and most thoroughly isolated convolutions of any animal[759].

[757] The want of symmetry is still more remarkable according to Tiedemann, in *Cercopithecus sabæus*, copied in *Icon. Zootom.*, Tab. vii. Fig. 4.

[758] See the beautiful figures of the brains of the ouran and chimpansee, in Tiedemann's work: *The Brain of the Negro, &c.*, Tab. vi. Sandifort has also given an admirable drawing of the brain of the Ouran, in the Trans. of the Society, *Der Nederlandsche Overseesche Bezittingen, &c.*, Heft. i.

[759] Figures of the dog's brain, in *Icon. Zootom.*, Tab. viii. Gall gives a drawing in outline of the brain of the elephant, *Op. Cit.* pl. xxxv.

§ 351. Before entering upon a comparison of the brain of the adult human subject, with the forms of this organ encountered in the mammalia, it is proper first to cast an eye towards the transitory forms of brain presented by the embryo or fœtus, at different periods of its development. The most cursory glance at early embryos of vertebrate animals, shows the evolution of the chief parts of the brain to proceed after one uniform plan. In the embryo of the fowl of the 30th hour (Fig XXXVI), the two posterior cerebral masses are already sketched out. The cell of the medulla oblongata or post-cerebrum (d^3), and of the corpora quadrigemina (d^2), thalami and third ventricle (d^1), which together constitute the meso-cerebrum, can be made out. About the 48th hour of the incubation, the pair of cells destined for the pro-cerebrum present themselves anteriorly in the guise of a couple of slight elevations; from these the olfactory nerve extends forwards and downwards; the olfactory lobes or mammillary processes of quadrupeds, are formed by an arrest of development of these anterior cerebral cells. These pro-cerebral parts gradually extend backwards and upwards, and finally come to over-lie the posterior cerebral parts, and the hemispheres are the product. The process of development is the same in all vertebrate animals, and in man. From the second cerebral cell the eyes are evolved, in the same way as the olfactory ganglia and mammillary processes, as immediate offsets from the brain. It is from this that the embryo of the fowl, and, indeed, embryos generally, appear hammer-shaped at this period. By and by, the eye-balls are pinched off, the optic nerves still presenting themselves as mere tubes of communication between them and the anterior division or meso-cerebrum (thalamus and third ventricle). The corpora quadrigemina advance in their evolution rapidly, and form a very large simple vesicle. In the two higher classes of vertebrata, and in man, this is a mere transitory form. But in amphibia and fishes, the corpora quadrigemina, which are already double, remain permanently of a large size. From the cell of the post-cerebrum (the fourth ventricle) the auditory vesicles are evolved, and in early embryos are observed as a couple of pediculated saclets connected with the cerebral part mentioned.

At this period there is no trace of the cerebellum to be seen. This part presents itself by and by, however, at first in the shape of a narrow bridge, as a production of the superior lateral band of

the medulla oblongata, spanning the floor of the fourth ventricle; and this is the form which we have seen the organ retaining through life in the naked amphibia. The pineal body is evolved as a small solitary lobule, and the infundibulum is produced inferiorly from the third ventricle.

In a perpendicular section, the roomy ventricles are seen extending into all the cerebral cells, from the ample canal of the spinal chord. We have noted such cavities and free communications as permanent forms in fishes.

§ 352. The HUMAN BRAIN, which interests us especially in this place, passes through the whole of the stages of development just enumerated, and undergoes still farther and more numerous metamorphoses till it attains its perfect state[760]. In human embryos of the second month, the grand divisions already indicated present themselves with sufficient distinctness, shining through the external coverings[761]. It is only at the end of the third month that the hemispheres take on the disposition to the extraordinary evolution which finally characterizes them. At this period the mass of the corpora quadrigemina, still of great relative size, remains completely uncovered. The cerebellum yet appears very narrow; the common cerebral ventricle on the contrary is very ample. In the fourth month, the hemispheres are growing larger, the several ventricles are becoming more distinct, the cerebellum is somewhat larger. In the fifth month, the posterior lobes of the cerebrum still remain rudimentary, and cover the corpora quadrigemina and cerebellum imperfectly; the lamellar structure of the cerebellum begins to be visible. At this period the transient or temporary form of the human brain bears some resemblance to the permanent cerebral form in birds, or of the lowest quadrupeds, such as the marsupians. In the sixth month, the posterior lobes grow with rapidity, and cover the cerebellum more and more; the cerebral hemispheres, however, are still smooth without any trace of convolutions, and the superior aspect of the brain is very similar to that of some of the smaller

[760] On the development of the fœtal brain, the work of Tiedemann on the subject still stands unsurpassed, 4to, 1816. Translated into English by Bennet, 12mo, Lond., 1826.

[761] See the representations of human embryos, Figs. lxxxv. lxxxvi lxxxviii. and xc.

monkeys. In the very ample lateral ventricles we discover corpora striata, cornua Ammonis, and the rudiments of the posterior cornua. In the seventh month, the hemispheres are well grown, and the rudiments of the future convolutions begin to make their appearance. The cerebellum is still but moderately developed. The formation of the cerebral convolutions once begun goes on rapidly. In the eighth month, in the course of which viable infants are first born, the greater number of the convolutions are already marked out, although they are still both fewer, shallower, and less decided, especially upon the superior aspect, than in the fœtus of the full time. The cerebellum is now divided into its several parts. The olfactory nerve, in its short and lobular form, reminds us of the permanent form of the part in mammals generally. In the fœtus at the full time,—at the end of the tenth month, the convolutions of the hemispheres appear as numerous and diversified as in the adult; the cerebellum alone, in point of relative size, is in arrear of the other parts[762]. With the second dentition, in the course of the seventh and eighth years the brain seems to attain its complete development in point both of form and weight, and its several parts now represent the relations which they preserve through the whole of after life[763].

[762] From some late researches on the brains of infants born at the full time, and that had lived for various short periods, I find the convolutions as numerous and asymmetrical as in the adult, nay, in some instances, the adult brain appeared to be less remarkable than the infantile brain in these particulars. The difference between one individual and another, in regard to the cerebral convolutions, would, therefore, seem to be already determined towards the end of the intra-uterine life. See Tiedemann, *On the Brain of the Negro*, p. 10. From the enquiries just alluded to, the brain of a new-born infant of the male sex appears to weigh between 13 and 14 ounces, that of the female infant from 9 to 12 ounces. Tiedemann also states, that the brain reaches its greatest size between the 7th and 8th year. The brain of a girl of 8 years 8 months old, he found to weigh 3 pounds 5 ounces and 5 drachms, which is about the mean weight of the adult female brain. (Vide § 395.) It is still a matter of doubt whether the brain diminishes in bulk in extreme old age. Tiedemann's inquiries would lead to the conclusion that it did.

[763] [This is surely a physiological error: on taking measurements of the head in 15 children between 7 and 8 years of age, I find the mean circumference to be 20¼ inches. But the mean circumference of the head in 10 children between 13 and 14 years of age in the same school, taken as they stood and without selection, is 21⅛ inches. If the size of the skull represent the size of the brain, therefore, the brain is not so large at 8 years of age as it is at 14; neither is

Whether or not any changes still take place in the more delicate structural relations is unknown[764].

§ 353. If we turn to the study of the brain and spinal chord with a particular looking to the nerves and their primitive fibres which enter and quit it, we very naturally come to the conclusion that the cerebral parts comprise within themselves the sum of the primitive fibres which are expanded throughout the body. And more particular inquiry shows us, in fact, that these fibres become more delicate in their structure, take their course through the interior of the brain and spinal chord, although in an imperfectly known manner,—here in bundles or medullary bands, there interwoven with masses of gray substance or ganglionic corpuscles. The mode in which these primitive fibres terminate in the central masses is still entirely unknown. The more essential points in this subject that have been made out, are these: the motory fibres of the spinal nerves enter by the posterior roots into the spinal chord, and whilst some of them take their course along the posterior bands or bundles of this part, others appear to penetrate its gray central mass, particularly upon the edges. They then proceed through the medulla oblongata, partly to the floor of the fourth ventricle, and partly as crura of the cerebellum, into the stem of the arbor vitæ. The rounded delicate strands proceed upon the floor of the fourth

it so large at 14 or 15 as it is at 20 and 25. On making the inquiry at several of the large hat shops of the metropolis, whether or not there was any difference in the sizes of hats required for boys of between seven and eight years of age and full grown men, I was assured that there was a very considerable difference; that the sizes for youths of 7, 8, and 9, were what are designated the $6\frac{1}{2}$, $6\frac{5}{8}$, and $6\frac{5}{8}$ sizes, whilst for grown men the mean average size is about 7, or from that to $7\frac{1}{8}$. The numbers here represent the mean between the long and the lateral diameters of the head. A London hatter says: "The head I have always found to attain its full dimensions in accordance with the bodily frame. I fix the utmost limit my experience will allow at 25 years. The more general period of full attainment of size is between 17 and 23. Many heads are at their full size at the age of 16." *Phrenolog. Journal*, vol. iv., p. 550, Edinb. 1827. R. W.]

[764] If we regard the gradual and much later attained development of the higher mental powers, we must admit the great probability of a gradual advance in the histological state of the hemispheres, up to the period of manhood, and farther, a degeneration in their constituent elements, with the advance of age. [The brains of children are never good subjects for anatomical demonstration—they are soft and pulpy, and do not bear handling like the brain of the adult. R. W.]

ventricle through the corpora quadrigemina, and the aqueductus Sylvii, and may be traced into the third ventricle. Of the anterior bundles of the medulla oblongata, the pyramidal bodies decussate in the manner generally known in the middle line, about an inch below the pons. The pyramidal bundles then pass through the pons into the crura cerebri, where they diverge and are readily followed into the thalami optici. The fasciculi composing the olivary and restiform bodies appear to take a similar course, their fibres running through the dark bluish grey coloured substance of the crura cerebri[765]. The precise manner in which these bundles and the primitive fibres which constitute them proceed subsequently is very imperfectly known, and their mode of terminating escapes us entirely. All that we have on the subject is mere hypothesis

[765] The issues of numerous and closely pursued investigations into the subject of the cerebral fibrillation, have to me been so unsatisfactory and so incomplete, that the few words given in the text are all I can venture on. Our anatomical knowledge of the connexion or continuity of the cerebral fibrillation, and the relations of the fibres of any part to the nerves that are connected with it, is still in its first infancy; but without advances in this knowledge, the function will remain as dark as it is everywhere else where anatomical data are wanting. [It strikes me, with great deference to my esteemed author, that the anatomy alone never tells us anything of the function. Who from seeing a particle of muscle under the microscope, and knowing its intimate structure most perfectly, could infer from this knowledge, that it would possess contractile power? Nay, is it not certain that we have long known the function of muscular fibre, but that we still dispute as to its precise structure? Who from examining particles of the retina and auditory nerves, could foresee that this would respond to impressions of light, that to the pulses of sound? The function of the liver has for ages been known to be the secretion of bile, but it is only yesterday that we are informed of its constitution by cells, and of the fact, that the nutrition and growth of these cells and the secretion of bile, are linked in the chain of necessary sequence, or are identical, and so on. All past experience seems rather to assure us that we shall never discover the function of a single part of the brain by taking the scalpel and microscope to it. R. W.] The works of Reil, l. c. 1807-8, et. seq. Gall and Spurzheim, *Op. Cit.* 1809, et. seq. *Physiognomical System*, 1815, and *Anatomy of Brain*, 1826; Burdach, *Op. Cit.*, 1819-26; Solly, *The Human Brain*, 1836; Le Gros Clark, *Anat. of the Brain*, 1836; Arnold, *On the Structure of the Brain and Spinal Chord*, 1838, and Valentin in Söemmerring's *Anat. of the Brain and Nervous System*, contain all the information extant on the anatomy of the brain. There is also an excellent short view of the entire subject by Heusinger in an addition to the German translation of Magendie's *Physiology*.

and contradiction, amidst which physiology finds no good foundation to build upon. It will be enough if we state generally here that recent inquiries seem to show: 1st, That the fibres of the hemispheres and their great commissure (corpus callosum) appear to have little anatomical connexion with the motory fibres of the spinal cord; 2nd, These motory fibres appear to end partly in the cerebellum and partly in the corpora quadrigemina and thalami. The anterior bands are, however, still to be followed through the corpora albicantia into the corpus callosum; 3rd, The primitive fibrils appear in the central masses, as well as in the periphery, to run side by side, but always isolated, never dividing and never anastomosing; 4th, The primitive fibrils appear to form the same kind of terminal loopings on the periphery of the several cerebral parts, as those of the nerves on the periphery of the parts of the body at large. This last point, however, must be allowed, by reason of the singular difficulty of the inquiry, to be anything but certain or demonstrated[765].

§ 354. The great diversities in point of size, and in the number and general appearance, of the convolutions of the brain in different individuals are very remarkable[766]. In men the brain is always on

[765] Valentin and Carus (*Physiol.* v. iii. p. 45) agree in stating, that the primitive fibres terminate in loopings on the periphery. Valentin has even given a representation of the structure which he saw, and which is copied in our Fig. CCXXVI, but Burdach, Remak, and Henle, have never succeeded in observing these terminal loops; and I have also myself generally sought for them in vain; it is only in the thalami of the pigeon that I have ever been able to perceive anything like the appearance which Valentin has represented.

[766] The convolutions of different brains appear to present interesting, and, as yet, little known, relations in point of general conformation [and position], vide Valentin's Söemmerring, p. 170. [Valentin dedicates four pages of very small type to this interesting subject; he refers particularly to the drawings of the brain, which we have from Söemmerring, Gall and Spurzheim, Rolando, (*Mem. de R. Ac. di Torino*, vol. xxxv,) and Arnold, and seeks to fix certain convolutions, or groups of convolutions, which are generally—I believe always—to be made out with a little practice, by appropriate names. I find, looking hastily down his pages, no fewer than 25 gyri,—convolutions or clusters of convolutions, thus particularized and appropriately named. In his concluding remarks, he says, "There can be no doubt that the study of the relations of the cerebral convolutions, in reference to configuration [and size] is of importance, both anatomically and physiologically. Although it is true, that the answer to the query, Whether or not they are the

an average larger than in women; in the middle period of life it is about one-fortieth of the weight of the body; frequently, however, it bears a much smaller relative proportion to the whole frame[767]. In cases of congenital idiotcy, the brain is generally obviously defective in size; frequently it has not half its proper dimensions[768]; the hemispheres, particularly in their anterior and posterior lobes, are developed in a very imperfect manner. Those individuals, on the contrary, who have been remarkable for their intelligence and force of character, have always been found to have large brains[769].

material expression of certain mental dispositions? still lies at so great a distance, that very certainly the present generation will not succeed in giving it any decisive solution, nay, will scarcely find itself in a condition to venture a well grounded opinion on the matter; still so much is quite certain, that they give outward indication of a great number of special variations in the configuration of the cerebrum. It were, therefore, a very meritorious undertaking, to give a series of carefully made outline drawings of different brains, and to describe them comparatively." It is rather curious to remark that this was the very task which Gall set himself when he began collecting casts and skulls half a century ago. R. W.]

767 The mean weight of the brain, according to Krause, is 48 ounces for the male, 44 oz. for the female. Tiedemann's work *On the Brain of the Negro*, already so often quoted, and so rich in matter, contains much information on the weight of the brain, according to age, sex, and individual. In 39 cases the weight of the brain of men between 22 and 80 years of age, varied from 2lbs. 8oz. 5dr. 50 grs. to 3lbs. 10oz. 2dr. In the majority of instances, the weight was from 3lbs. 5oz. to 3lbs. 8oz.

768 In an idiot 50 years of age, the brain weighed only 1lb. 8oz. 4dr.; in another aged 40, it was 1lb. 11oz. 4dr. in weight, and in a third, aged 16, it was no more than 1lb. 6oz. 1dr., Tiedemann, l. c.

769 The brain of Cuvier, for example, weighed 4lbs. 11oz. 4dr. 36grs.; that of Dupuytren 4lbs. 10oz., Tiedm. l. c. p. 9. In none of the cases above quoted have we the proportion to the weight of the body, which is of consequence. Tiedemann found it to vary from 1 in 37 to 1 in 46; in the mean, 1 in 41 or 42. The female brain, although absolutely smaller than the male brain, nevertheless bears the same relative proportion to the body. The brain of the Negro and other inferior races does not appear to be any smaller. The brain of idiots appears to be altered in its other relations likewise. Unfortunately, however, we have but few inquiries upon this topic, which is of the very highest interest. Jaeger of Stuttgardt made a very important contribution to the history of individuals with defective brains, very lately, (vide *Medicinsches Correspondenz-blatt des Würtembergischen ärztlichen Vereins*, B. ix. No. 28). In a boy of 10, whose head was not larger than that of a new-born infant, the brain was of

These differences are of course proclaimed in the size and shape of the skull; whence, in idiots, we have the low and narrow forehead, and the disproportion between the cranium and face, proclaiming the deficiency of brain[770]; whilst, in the man of capacity, we have the roomy skull, of a rounded or oval shape, as an indication of the size of the mass which it incloses and defends[771]. In the same way the more nobly constituted and civilized races of men are distinguished from the lower and more savage tribes by the greater size of the cranium, both absolutely and relatively, to the size of the face[772]. It has also been observed that in men of the highest mental endowments, both the number of the convolutions and the want of symmetry

remarkable firmness; no alteration in the convolutions was remarked, but no other brain was used for comparison. The lateral ventricles were small; the left corpus striatum was two-thirds smaller than the right one, and flatter. The thalami which were of an elongated figure, were most intimately conjoined through their whole length, so that there was no third ventricle; the posterior commissure was also wanting. The pineal gland lay very far backwards, and the concretions commonly formed in its interior were wanting. The corpora quadrigemina were much smaller than natural, and completely fused together. There was no fourth ventricle. In the cerebellum, various abnormal conditions were also observed.

770 See drawings of such skulls of idiots, which are very remarkable, and afford cranioscopy some of its very strongest points, in Blumenbach, *De anomalis et vitiosis quibusdam nisus formativi aberrationibus*, Gotting, 1813. Sandifort, *Museum Anatomicum*, vol. iv. where the brain is also represented, and Owen, in *Trans. Zoological Society*, vol. i.

771 Gall—*Physiologie du Cerveau*, tom ii., p. 20, gives many instances of large size of the skull in men of talents. See also the figure of the skull of Fried. von Schiller in Carus's *Outlines of a new Cranioscopy on a Scientific basis—Grundzüge einer neuen und wissenschäftlich begründeten Kranioskopie*, Stuttg. 1841. Noel—*Outlines of Phrenology—Grundzüge der Phrenologie*, Dresd. 1841, gives a drawing of the head of Michael Angelo, contrasted with that of an idiot, in his first plate. [At a great metropolitan hat shop, I am informed that the fine hats worn by the wealthy and educated classes, are manufactured on an average of one and two sizes larger than the coarse and commoner hats worn by the labouring classes. A *groom*, a *stable boy*, and a *coachman*, have all but invariably small skulls; nine in ten of these men will be fitted by hats of the $6\frac{5}{8}$ and $6\frac{6}{8}$ sizes. A *footman*, on the contrary, generally requires a hat of the 7 or full size. R. W.]

772 Vide Blumenbach's *Decades Craniorum*, and the series of skulls, in Tab. ii. and iii. of my *Icones Zootomicæ*. Many of the heads of idiots, in point of cerebral development, do not surpass those of some of the higher monkeys—the chimpansee, for example.

between those of the two sides were more than usually remarkable[773]. In individuals nowise distinguished by their mental powers, on the contrary, and in the inferior races generally, the convolutions have been found decidedly fewer in number and more symmetrical, particularly in the front halves of the hemispheres[774]. It has also been held that congenital inequalities between the hemispheres were unfavourable to the perfect manifestation of the higher faculties of the mind[775].

Functions of the Brain and Spinal Chord.

§ 355. We are accustomed to speak of the brain and spinal chord as the centres of the nervous system, because the whole of the nervous functions have here their point of reunion, their source, or their seat[776]. Here all the centripetal nervous chords unite; in the brain are the sensations of all the peripheral parts perceived with their appropriate qualities; and, on the other hand, from the brain and spinal chord does the stimulus that excites muscular motion of every description take its departure. The latter fact we ascertain more immediately and strikingly from the voluntary motions, less so from those that are merely automatic. The nerves seem to serve as mere conductors of the nervous influence, which appears to be incessantly engendered in the brain; it is on this account that the activity of the nerves, their faculty of reacting on the application of

773 In the brain, for instance, of Cuvier, Dupuytren, Döllinger.

774 Among Negroes and the Bushmen, see Tiedemann, and my *Icon. Zootom.* Tab. viii.

775 See Demme's inaugural dissertation, *On inequalities in the two hemispheres of the Brain*, Würzb. 1831. This malformation appears to be more frequent among men than women. [In a greater or less degree, it is almost universal—scarcely any individual has the two sides of the head precisely alike, and the same may be said of the lower animals. Bichat laid much stress on the unfavourable influence of inequality in the two halves of the brain; his own skull was, however, much larger on one side than the other. R. W.]

776 In this and the paragraphs that immediately follow, I have confined myself to the merest outlines of the subject; this at the present moment may be held to be the part of physiology which is the most in want of illustration, and that is more intimately mixed up with hypothesis than any other. Without a lengthened critical examination of all the more recent views and assumptions of the many and constantly contradictory writers which we have, it would be impossible to give a general and comprehensive summary of the physics of the nervous system.

stimuli, is speedily lost when their connection with the central parts is destroyed, § 241. The motory power of the nervous influence either flows incessantly from the central parts to the muscles, as in the case of the sphincters, which lose their tone and relax when their nervous connection with the central parts is interrupted; or it flows in rhythmical waves, at regular intervals, as in the case of the respiratory muscles; or otherwise it only passes out at the immediate behest of the soul, as in reference to the whole of the voluntary muscles[777]; or, finally, in consequence of an internal excitement or shock given to the brain by peripheral impressions received through the medium of the centripetal nerves, a centrifugal reflux of the nervous influence is induced, and certain motions take place independently of volition. These motions belong to the much diversified class of reflex or reflected motions, which present many peculiar and very interesting phenomena to our observation[778].

It seems probable, although at the present moment it is not demonstrable, that all the operations of the brain upon the nerves and effected through their medium, depend on an influence of the gray substance upon the primary fibrils; were this proven, the ganglionic

[777] For the reasons just assigned, I have avoided in the following paragraphs all discussion of the higher psychological functions. All that can be said on this subject is met with in our ordinary elementary works, in the shape of reasonings, or examples, without reference to any definite general principle. The most able consideration of this topic, as well as of the doctrine of the nervous functions at large, that I have seen, is contained in Henle's *General Anatomy*, p. 680 et seq. I shall have occasion to revert to it in the general physiology.

[778] The phenomena, which, under the title of reflex functions, have lately attracted so much attention, and have been held of such importance, were familiar to the older physiologists and physicians. For the systematic development of the doctrine of these phenomena, however, and a knowledge of the laws which govern them, we are indebted to our own times. Dr. Marshall Hall, in England, and Prof. Jo. Mueller, in Germany, independently of each other, erected the theory of reflexion (see § 242, and Annots.) Many physiological and pathological motory acts belong to the category of reflected motions, which may be exhibited in a multitude of experiments, and these by an analysis of the phenomena which occur, may readily be varied and still farther multiplied. Among the number we reckon the motions of the iris from stimulation of the retina, already spoken of, sneezing, swallowing, coughing, vomiting, many kinds of clonic spasm, in which the brain and spinal marrow are not primarily affected, as for instance in teething, from worms in the intestines, &c., also the tonic spasms that follow injuries of the extremities, starting on the occurrence of sudden noises, &c., &c.

corpuscles would have to be viewed as the proper productive organs of the nervous influence.

§ 356. If we inquire in the first place into the simplest conditions in the organization of the central parts with which the vital processes are compatible, we discover that the spinal chord is of itself sufficient, even in man and the higher vertebrate animals, to support life, at least during the fœtal period of existence. In cases of imperfect development of the superior or anterior half of the body, or of the head—acrania, anencephalia—the brain is entirely wanting; the spinal cord (and medulla oblongata?) and the nerves which proceed from it, are alone more or less perfectly formed. The other parts of the body, the extremities, the trunk, and its included viscera, may be present and well developed, though it often happens that they too are either partially wanting or imperfectly formed. From this condition we observe every degree of progressive completeness as we proceed through the various grades of defective brain—microcephalia, up to the perfect evolution of the hemispheres, so that we become certain that the embryo may attain its complete development without the presence of any brain, and that the child may even live for some short time after its birth in this state. In all such cases, however, the medulla oblongata, with the nerves that proceed from it, appears always to have been present[779]. Fœtuses at the full time, whose crania have been perforated and the brain in great part removed to admit of their passage through the contracted pelves of their mothers, have nevertheless in some cases breathed, cried, and moved their extremities after their birth[780]. These pathological facts have their parallel in comparative anatomy. The amphioxus

[779] Meckel treats the subject of monstrosity with greater completeness than any other writer, in his *Pathological Anatomy*, vol. 1, p. 140. It must be allowed that in the greater number of the accounts which we have of cases of acephalia, such an anatomical description as would meet the present requirements of physiology, is wanting. Spezza lately gave a description of an anencephalic fœtus which lived 11 hours after its birth. The brain, cerebellum, and medulla oblongata were all absent; the spinal marrow began superiorly in the skin of the neck, with a papilla the size of the point of the little finger, which Jo. Müller regards, with justice, as the medulla oblongata, inasmuch as an acceleration of the respiratory motions, and some crying and sobbing, followed stimulation of this part during life. We cannot suppose, indeed, that without a medulla oblongata there could be anything like respiratory or vocal movements. (Spezza, *Gazette Medicale*, Janvier, 1833).

[780] Vide Mueller's *Archiv.* 1834, p. 168, and the *Journal of the Berlin Medical Union*, No. 22.

lanceolatus, a genuine vertebrate animal, a fish, besides being completely acephalic, or having no proper skull, has only a spinal marrow, no part presenting itself as distinct from this which might be called a brain. The nerves are all alike, and fashioned after the type of the spinal nerves generally; the most anterior only, which is of somewhat larger size than the rest, may be assumed from its divisions as corresponding to the nervus trigeminus. The spinal marrow, in this most remarkable and lowest of all vertebrate animals, ends anteriorly and posteriorly in a sharp point; in its interior, however, it contains gray matter in the centre,) medullary substance in the periphery ?) The skeleton in this creature consists essentially of that part which first makes its appearance in the embryos of all vertebrate animals, the chorda dorsalis, which is here persistent, as indeed it is in other fishes of the lowest grade, but which disappears in all the higher animals of the order after the formation of the vertebral column. Besides this simple skeleton, there is also a muscular system, an intestinal canal, without any accompanying glands, a respiratory organ, urinary organs, several distinct hearts (an aortic heart, a heart of the portal system, and a heart of the vena cava), and male and female organs of generation divided between different individuals[781]. From this we have the assurance that a certain sum of organization, such in short as appertains essentially to the class of vertebrate animals, may exist without a brain, or at least with no more of the central nervous mass than is represented by the medulla oblongata, and that such an animal is capable of independent existence, although of course in the most limited rela-

[781] We have two monographs of recent date upon this remarkable fish, which was known to Pallas, but has but just been duly described. One is by Rathke, *On the Structure of Amphioxus lanceolatus*, *Ueber den Bau des Amphioxus lanceolatus*, Königsb. 1841; the other is by Jo. Müller, who had the animal alive, and communicated his observations in the monthly notice of the proceedings of the Berlin Academy, Dec. 1841. Another remarkable peculiarity of this creature is, that its blood is colourless. The amphioxus belongs to the order of cyclostomous fishes, and appears to occur in all the European seas. We must conclude that the anterior extremity of the spinal marrow is a true, although it may be an imperfectly developed, medulla oblongata. [Mr. Goodsir, of Edinburgh, has added another excellent monograph upon this curious animal, which will be consulted with interest, vide *Trans. of the Royal Society of Edinb.* vol. xv. part 1, 1841. Mr. Goodsir is of opinion that the creature has literally no part analogous to brain. The spinal cord is totally destitute of primitive fibres; it consists alto-

tionship with external objects[782]. The structure of this animal is a very remarkable and important fact for physiology at large.

§ 357. In every other vertebrate animal, as in man, we find a brain developed on the anterior extremity of the spinal cord. The spinal cord is in relation with the whole of the nerves of the trunk, and like the brain consists of ganglionic matter and primitive fibres. Its functions in general, not in especial, are the best known of those of any of the central masses, although we are still receiving almost daily contributions to its anatomy and physiology. The spinal cord proclaims itself to be as well a central as a conducting organ. In this latter respect it is therefore on the same level with the nerves, for it certainly conducts impressions received in the periphery to the brain, and transmits the desires of the brain to the periphery. The former are passed through the sensitive fibres or posterior nervous roots, the latter through the motory fibres, and exclusively by the anterior nervous roots (§ 237 and 262). The spinal chord has, however, and as it would appear exclusively in virtue of the gray matter in its composition, or the ganglionic cells collected in its interior, certain properties which characterize it as a central organ, and raise it in some sort to the rank of the brain. It has a proper inherent motory power, which it communicates to its nerves independently of the brain; a fact which is proclaimed especially by the state of tonicity or permanent contraction of those muscles, the sphincters, to wit, which depend most immediately on the spinal cord [82]. The spinal cord also exerts specific influences upon certain organic functions. The acts with which it is in relation, however, are not associated with consciousness. If the brain be separated from the spinal chord in a frog, the animal will nevertheless go on for hours possessed of the power to move its extremities, when any part of the integument is pinched or stimulated, but without all consciousness, and

gether of isolated cells, arranged in a linear direction only towards the middle of the cord. The nerves originate by single roots, the primitive fibres of which they consist being seen to approach close to the cellular mass of the spinal cord, but without passing into it. R. W.]

[782] The contraction of certain muscles during life, such as the sphincter ani and sphincter vesicæ urinariæ, depends on the spinal chord. The sense of weariness, and the paralysis of the lower extremities that follow excesses in sexual indulgence, give us additional assurance of the existence of a special motory power resident in the spinal chord.

without anything like volition; the motions are automatic, and proceed directly from the spinal chord, in consequence of an excitement or stimulation of its substance effected through the nerves of sensation; the motions are pure reflex motions; in other words, motions which arise from stimuli conveyed to the spinal chord by centripetal or incident nerves, which stimuli are then transmitted from the chord to centrifugal or excito-motory nerves[783].

§ 358. The best subjects for the study of the influence of the spinal cord upon motion, are decapitated animals, naturally tenacious of life, such as frogs[784], which, indeed, seem peculiarly fitted for experiments on the reflex motions. If a decapitated frog be placed in a suitable and as nearly natural position as possible, it will be seen that the animal has no power of moving, save under the influence of external stimuli; the capacity by an internal motion or volition to move any of the parts supplied with nerves from the spinal chord has ceased with the removal of the brain[785]. Immediately after decapitation, very violent convulsive movements follow in the trunk and extremities of all animals, in consequence of the pressure and violence attending the incision. Occasionally, but not

[783] The organic function above referred to, with which the spinal chord stands in a kind of specific relationship, is the sexual system. Nutrition and the power of engendering heat, suffer from over-indulgence of the sexual appetite; the skin falls in a state of diminished vital turgor, the digestive process fails, &c. [Probably the affection of the nervous system is quite general. In cases of paralysis of the lower extremities, in consequence of injuries of the spine, the secretion of the urine seems always to be implicated—the fluid is pale and watery, and either neutral or ammoniacal. R. W.] Besides the works already noticed, on the anatomy and phsyiology of the nervous system, we have lately had Longet, *Recherches exper. et pathol. sur les proprietés et les fonctions de la moelle epinière et des racines des nerfs*, Paris, 1841; Stilling, *Fragments on the subject of the Functions of the Nervous System,—Fragmente zur Lehre von der Verrichtung des Nerven-Systems, in Roser und Wunderlich's Vierteljahrsschrift*, 1842, and separately.

[784] Amphibia are the only good subjects for such experiments; tortoises and serpents are preferable to frogs in some circumstances. The irritability is too speedily quenched in warm blooded animals; nevertheless, all the phenomena observed in frogs may also be demonstrated in them. Frogs are particularly susceptible in spring and autumn, and also in winter, even after they have fasted for a very long time; they are less excitable in the great heats of summer.

[785] Vide § 343. With the pliers there described, the whole skull may very readily be removed, and the brain partially or entirely taken away. Some short interval must be allowed to pass after such an operation, as well as after decapitation, before any experiment is made.

often, the decapitated frog will make a vigorous spring immediately after the operation[786]. In the severed head we frequently observe chewing and swallowing motions, consequences doubtless of the violence done to the medulla oblongata. Once all has fallen into a state of repose, the trunk remains in the position in which it is placed, if stimuli of every kind be avoided; not a limb moves, not a muscle quivers[787]. Frogs and other amphibia will remain in the same position, motionless for hours, and yet on the application of a stimulus they may be made to move again. If, however, the frog be placed in what might be called an incommodious posture, immediately after the decapitation, and when everything like convulsive movement has ceased,—if the hind leg, for instance, be stretched out behind the animal, it will by and by, within from five to ten minutes, be spontaneously drawn up under the body, as it is in the usual sitting position of the animal. This movement is probably an effect of the sense of dragging and stretching, familiarly known to be experienced in parts placed for some time in a constrained position; the sensitive nervous fibres of the parts so stretched are irritated, the irritation is transmitted to the spinal chord, and a reflex movement ensues; the motion of placing the hind leg as it is in sitting is therefore by no means to be viewed as an act of volition, or as done with consciousness on the part of the headless animal[788]. Motions, on the other hand, follow immediately upon the application of stimuli almost of any kind, which must be even as involutarily and unconsciously performed, as those just considered. These motions are varied according to the part that is stimulated, and the extent and intensity of the stimulus employed. The skin of the frog is abundantly supplied with sensitive nerves, and reflex pheno-

[786] Vide § 401, and Annot.

[787] Kürschner in his translation of Marshall Hall, recommends the decapitated animal to be covered in the first instance with a glass shade, and before any stimulus is used; and all shaking of the floor or table on which it is placed must be avoided, such succussions being sufficient to give occasion to reflex motions.

[788] Kürschner and Volkmann have made this readily verified observation, and explained the nature and cause of the motion described. The leg is drawn suddenly, not gradually, under the body, so soon as the exhaustion consequent upon the decapitation has passed; it is generally the first sign of the restored susceptibility to stimuli. Vide Kürschner, l. c., p. 132.

mena are most certainly induced by employing cutaneous stimulation[789]. If, for instance, a drop of acetic acid be applied to any part of the skin, or if the same part be pinched with the dissecting forceps, we never fail to see certain complex motions follow, which continue for a variable length of time, are of greater or less extent and intensity, and have this remarkable peculiarity also, that they seem to stand in a kind of necessary connexion with the part of the skin which is irritated[790]. We never observe respiratory motions in the course of such experiments, when the medulla oblongata is entirely removed[791]. Neither are any regularly combined movements executed, an extensive harmoniousness of action between the muscles of the trunk and of the anterior and posterior extremities being necessary to such acts; we even perceive in the mode of holding itself, of the decapitated frog, a want of that balance and force which are conspicuous in the unmutilated animal; the trunk in particular is bent downwards towards the belly; the fore legs are more drawn up and do not seem to serve as supports in the usual way. The balance between the flexor and extensor orders of muscles is destroyed, and the alternation of action between antagonist groups is either much diminished or totally lost[792]. The extent and vigour of the

[789] The most irritable parts of the skin are those about the articulations, upon the sides and over the belly; the integument of the back is less susceptible. Reflex motions are induced with much greater difficulty by stimulating the muscles; in consequence of their deficiency in sensitive or incident nervous fibres. The respiratory and digestive organs seem also to transmit stimuli applied to them in decapitated animals generally, with great difficulty to the spinal chord; whilst in living animals, man and the mammalia especially, so many stimuli applied to the mucous membrane of the respiratory and digestive systems give occasion to reflex movements; here the integrity of the central parts would therefore appear to be necessary.

[790] It is very interesting to see the same motions always following the same irritations of the skin. If the integument of the right side be stimulated, the frog immediately raises the corresponding hind foot, and seeks to reach, and as it were to remove, the cause of the irritation; so also in reference to the left side. Stimuli applied in the mesial line, to the anus for instance, occasion movements in the limbs of both sides.

[791] Vide Kürschner, l. c., p. 140. No expansion of the chest follows stimulation of the skin covering it, nor of the bronchial mucous membrane, nor even of the spinal chord directly, although the trunk is then often turned in all directions. [As the frog inflates its lungs by the action of the muscles of the lower jaw and os hyoides, no expansion of the chest can take place in this animal when its head is struck off. R. W.]

[792] Vide Kürschner, l. c., p. 144, who states very correctly, that extensors,

motions are also constantly very decidedly implicated by the removal of the brain[793]. It is at this time doubtful whether or not any of the organic functions, secretion for example, are renewed upon the application of stimuli to decapitated animals[794]. The motions which follow stimulation in decapitated animals continue for a longer or shorter space of time, according to the nature of the stimulus, and in a general way are clonic in their character; it is only in connection with very violent stimuli that they become tonic; tetanus, however, may be induced by the application of the galvanic stimulus of high tension, as also by poisoning with strychnine previously to the occurrence of paralysis[795]. The most diversified motions occur upon the direct irritation of the spinal marrow by the use of a fine needle at the place of division. Here we have an opportunity of testing the remarkable fact, that motions never ensue upon stimulation of the posterior columns of the chord, whilst they as certainly follow the application of the needle to the anterior columns. The consequences are unequal and uncertain when the grey substance is pricked. These experiments may be repeated with the same invariable results upon different sections of the chord, higher up or lower down in its course[796].

flexors, abductors, adductors, and various other muscular groups, may be active in an extremity, but that everything like very complicated motory acts are impossible after decapitation. Flourens had already directed attention to this fact. Although motions occur, therefore, simultaneously in the trunk generally, and in all the extremities, they are on the whole rather spasmodic or convulsive throes, than regular coordinated movements. The trunk often shifts its place turning in a half-circle round, but the motion is not one of those effective leaps which the animal performs in its state of health, and with its medulla oblongata entire.

793 As I find in accordance with Flourens and Kürschner.

794 Kurschner makes a statement which I have not been able satisfactorily to verify, viz: that in decapitated frogs, the skin will become moist upon the application of stimuli, and that in cases in which he had made use of sulphuric acid to the skin, the surface became bedewed with a frothy fluid.

795 Slight irritation of the spinal chord with a needle, or with a simple pair of plates, produce clonic spasms only; a more powerful galvanic apparatus causes tetanus; which may also be induced in decapitated frogs by the poison of strychnine.

796 Vide Kürschner, l. c., p. 197. I may here observe, that I can vouch for the accuracy of the experiments of Kürschner, which give a very clear and satisfactory view of the functions of the spinal chord, quoted in this paragraph, and

§ 359. From the experiments quoted at the close of the preceding paragraph, it may be inferred, that the posterior and anterior bundles of the spinal cord comport themselves in the same manner as the nervous roots that are severally connected with them; that the posterior tracts are purely sensitive, the anterior purely motory. A very different question, however, is that which requires to know the function of the several parts of the grey substance, and their reciprocal influence upon the anterior and posterior bands of the chord which are composed of white matter. Unfortunately the views of the most distinguished experimental physiologists are here entirely contradictory. It is for time and renewed inquiry to reconcile their differences[797]. Even the more intimate structure of the spinal cord is not yet very exactly ascertained[798].

that I can agree with him in the inferences he draws. The functional relations of the several tracts or strands, and particular substances of the chord, as they are set down by recent observers, which yet remain to be spoken of in the next ensuing paragraphs, appear to me to be still in some measure problematical; the views and statements are everything but accordant; and my own experiments do not enable me to come to any definitive conclusions. Some of the experiments of distinguished inquirers must only succeed with precautions and arrangements to me unknown. Stilling, for instance, l. c., p, 125, says, "If the spinal canal of a frog be laid open from behind, by taking away the third and fourth vertebral arches, and the spinal chord be then divided at the distance of a line under the point at which the roots are given off to form the nerves of the anterior extremity, and a drop of acetic acid be now applied to one of the fore feet, the hind foot of the same side will be used to remove the irritating fluid from the fore foot precisely as if the animal were uninjured." I have tried this experiment on 20 vigorous frogs, in winter and in spring, but without success. The circumstance would indeed be very remarkable could it be confirmed.

[797] I shall do no more here than give a summary of the conclusions come to by different experimentalists as set down by themselves at the end of their treatises, without going into the detail of their several experiments. The chief difficulty experienced, I may mention, seems always to have been to limit the trials to particular isolated portions of the spinal chord, without implicating other parts in connexion with them. According to Van Deen, l. c. p. 199, the functions of the spinal chord are these: 1. The white or medullary tracts of the anterior fasciculi serve for motion alone. 2. The anterior fasciculi with their grey substance serve for sensation as well as motion. 3. The white substance of the posterior columns serves for sensation alone. 4. The posterior columns with their grey substance are still destined exclusively for sensation. 5. The white substance of the posterior columns need not necessarily extend to the brain in order

§ 360. The MEDULLA OBLONGATA ought undoubtedly to be considered as an integral part of the brain; but both on anatomical

to communicate there the impressions received by the channel of the anterior nervous roots. 6. The white substance of the posterior columns does not of itself readily transmit sensitive impressions to the brain. 7. But the white substance of the posterior columns, so long as it is in contact or communication with its grey matter, transmits impressions to the brain with ease. 8. The anterior white substance without the grey substance is not capable of conveying the dictates of the will directly to the muscles through the anterior nervous roots; it can at most induce muscular twitchings or convulsions. 9. The same conditions that excite sensations also occasion reflex motions, that is to say, that as sensation depends on the posterior columns, grey matter, and nervous roots, so does the reflex motion depend on the same parts of the spinal chord. 10. In the same way as the anterior columns convey sensation to the brain do they also occasion reflex motion in the direction of the spinal chord to the brain; neither ensues, however, without the co-operation of the grey substance. 11. It is through the grey substance that impressions from the posterior roots are communicated to the anterior roots. 12. It is also through the grey substance that impressions from one centripetal primitive fibre are communicated to another. 13. The grey substance performs the same office with regard to the centrifugal primitive fibres. 14. The centripetal and centrifugal [incident and excito-motory] fibres must be viewed as mere conductors of the nervous influence; the grey substance as the active centre of the nervous system.—Stilling (l. c. p. 143,) from his experiments deduces the following conclusions: 1. The posterior nervous roots are sensitive, but this they are solely through the posterior grey matter, and their connexion with the posterior columns. 2. The posterior white or medullary substance, or posterior columns, are sensitive only in virtue of their connexion with the posterior grey substance. 3. The posterior grey substance is alone capable of transmitting sensation from the seat of consciousness to the brain. 4. The posterior medullary substance alone is not capable of transmitting sensation to the brain. 5. The anterior medullary substance or anterior columns are, in common with the anterior nervous roots, insensible. 6. The anterior columns alone are not capable of transmitting the behests of the will to the motory roots. 7. The anterior grey substance is alone capable of communicating the influence of the will directly from the brain, and by the means of the anterior columns to transmit this farther, viz., to the motory nervous roots. 8. There is no necessity for the uninterrupted connection of the posterior columns in order to have impressions conveyed to the brain, nor is there any necessity for the uninterrupted connexion of the anterior columns to have the dictates of the will transmitted to all parts of the spinal cord. 9. The dynamic changes made in the posterior grey substance by impressions received, extend farther in all directions in the course of the length and of the breadth of the chord in every sense, consequently upwards to the brain, whence results sensation, anteriorly to the anterior grey substance, whence ensue reflex motions, from one side to another, whence follow more extensive consentient movements even in the side of the body not originally impressed,

and physiological grounds it must be viewed as sharing its functions with the spinal chord. The very great importance of this cerebral part also appears from the fact, that the whole of the cerebral nerves, with the exception of the two first pairs, are in immediate connection with it. It stands to these in the same relation as the spinal chord does to the spinal nerves. It is here too that the anterior columns of the spinal cord decussate, viz., at the apices of the pyramidal bodies. The decussation appears to stand in a kind of special

and so on. 10. Impressions made on the posterior columns, like those made on the anterior columns, do not extend farther lengthwise along the spinal chord. The impressions of the posterior columns proceed from behind forwards, in a horizontal direction, to the posterior grey substance. The impressions of the anterior columns pass over to the nearest motory roots. 11. To the production of sensation, the uninterrupted connection of the posterior grey substance betwixt the part irritated and the brain, is necessary; to the excitement of voluntary motions, the uninterrupted connection of the anterior grey substance betwixt the brain and the nervous root that is called into action, is indispensable.—Budge (*Researches on the Nervous System,—Untersuchungen über das Nerven-System*, p. 12. et seq.) announces the conclusions from his experiments as under: 1. There is no level or point in the whole thickness of the spinal chord that is without sensation,—it has its seat in the length, in the breadth, in the middle, and to either side, before and behind,—everywhere there is sensibility. 2. Sensation is much more acute in the outer layer of the posterior columns of the spinal chord than in the outer layer of the anterior columns. This layer removed, however, the susceptibility to impressions of pain is nearly everywhere alike. 3. The sensitive fibrils continue through the entire length of the spinal chord upon the same side,—those of the right to the right, those of the left to the left. 4. The sensitive fibres which together have their entrance from the posterior aspect of the chord, must, necessarily, having entered the organ, proceed to the anterior aspect, else could there be no sensation in connection with them. 5. The motory fibres run through the whole thickness of the spinal chord,—they lie behind, before, inside and out. 6. The motory fibres of the whole of the trunk and extremities being collected in the anterior aspect of the spinal chord, the motions which follow the irritation of this aspect are of course more powerful; but the capacity to perform motions is implicated in the same degree, by the destruction of a portion of the posterior columns, as it is by the destruction of a portion of the anterior strands. 7. Motions in extension can be excited from a larger extent of the spinal chord than motions in flexion. 8. The nerves which preside over motions in extension predominate in the anterior strands of the spinal chord. 9. The nerves which are connected with motions in flexion, predominate in the posterior aspect of the chord; but they are not there alone.

[793] I have not, at all events, been able to make out the relations between the ganglionic corpuscles and the primitive fibres.

relationship with the motory fibres of the inferior extremities[799]. The medulla oblongata is a very principal apparatus of motion; any stimulation or irritation of its substance is followed by convulsive movements of the whole body, upon which paralysis ensues. It is an especial reflector, and of all parts it is that which is most extensively connected with reflex motions; peripheral irritation or stimulation of the nerves which arise from the medulla oblongata, is peculiarly apt to induce reflex motions. The most important motory influences, however, of the medulla oblongata are those that subserve respiration, which, indeed, depends exclusively upon it; respiration immediately ceases when it is injured. All the rhythmical motions associated with the act of respiration, such as laughing, yawning, sighing, etc., likewise depend on the medulla oblongata. The faculty or power of volition seems also to have its probable seat in the medulla oblongata; for many of the inferior vertebrate animals, after the partial or complete removal of their brain and cerebellum, still retain the power of performing voluntary motions; notions which at all events, from the combination required in them, and number of muscles brought into action, have every semblance of voluntary[800]. All the psychological excitements or faculties,—affections, passions, etc., are realized or made manifest by means of the medulla oblongata, and all the more extensive motions,—locomotion, etc., are only possible along with perfect integrity of this part[801]. It still remains doubtful in how

799 According to Budge, (l. c., p. 22,) the decussation of the motory fibres of the lower limbs take place in the medulla oblongata; the corresponding fibres of the upper extremities have not yet decussated here. The decussation of the nerves of the inferior extremities appears from experiment to take place at no great distance from the end of the medulla oblongata, and not, or in a very trifling degree, only at the entrance into the cavity of the cranium. Experiments on the medulla oblongata are undertaken precisely in the same way as those already described in connexion with the spinal chord of the frog (§ 358).

800 This conclusion is from the enquiries of Flourens, although the experiment is hardly to be made in such a way as will enable any certain distinction to be made between voluntary and involuntary motions. The indisputably voluntary motions of the amphioxus lanceolatus give us better assurance that the thing is so, for if there be any central nervous part other than the spinal chord developed in this curious animal, it is the medulla oblongata. Vide § 356.

801 Stimuli applied to the integuments of decapitated frogs, only cause the animals to leap, when the medulla oblongata still remains connected with the trunk and uninjured, a fact which is easily ascertained by experiment. Kürsch-

far the medulla oblongata participates in the faculty of sensation. Any conclusion in this direction from experiments must be unsatisfactory, inasmuch as all the phenomena that have been noted are readily referred to reflex actions[801]. The exposure and injury of the medulla oblongata in living animals appears to be one of the most painful operations that can be performed[802]. The pons is also extremely sensitive; the walls of the aqueduct of Sylvius, on the contrary, seem to be altogether without feeling[803]. The pons, moreover, receives very numerous motory fibres from the anterior strands of the medulla oblongata.

§ 361. The cerebellum gives no indication of being possessed of feeling when its superficial parts are taken away. The deeper parts, however, do appear to be sensible, although the results of vivisections are very contradictory on this point[804]. The consequences of removing the cerebellum, indeed, seem to differ somewhat in the different orders of animals; still the results are far more generally accordant than we are accustomed to find them in experiments upon other central parts of the nervous system. When smaller or larger slices are taken from the cerebellum, the power to execute definite locomotive acts is always either lessened or totally lost. A state is induced which bears some resemblance to that of intoxication, in which, indeed, from analogy with what we see in experiments on animals, we should conclude that the cerebellum was peculiarly affected. Animals whose cerebella have been injured or removed, acquire an insecure and tottering gait; they turn round, they move to the right, to the left, backwards and forwards, the faculty of balancing the body is lost, but the power of volition does not seem to be affected, for the creatures make a number of violent but use-

ner never saw any proper locomotion when the spinal chord only was left, l. c., p. 147.

801 The same observation may be made here as above, Annot. 799.

802 It is, therefore, well in performing such an experiment, first to remove the hemispheres, and so destroy consciousness.

803 See Magendie's *Lectures on the Nervous System*, p. 160. The slightest touch upon the anterior edge of the pons in the rabbit, occasioned every indication of the severest pain; the walls of the aqueductus Sylvii, again, when touched with a probe, appeared insensible.

804 According to Flourens and Hertwig, the cerebellum is insensible. Magendie, from experiments on rabbits, concluded that the superficial parts only of this mass were without feeling; deeper wounds caused indications of suffering.

less motions; they endeavour to escape; they try to avoid blows aimed at them; but they are efforts only that do not enable them to effect the purpose obviously desired[805]. These results have

[805] The numerous and always accordant conclusions of experimenters upon this point are satisfactory. The first fundamental and very comprehensive experiments were made by Flourens, on animals of different orders, but particularly on birds (*Recherches exper. sur les propriétés et fonctions du Système Nerveux*, 1824, *et Experiences sur les Système Nerveux*, *suite aux Recherches*, 1825). His experiments were repeated and confirmed by Hertwig, (*De effectibus læsionum in partibus encephali*, Berol, 1826,) and by Budge, *Op. Cit.*, Part i. Flourens removed the outer layer of the cerebellum of a guinea-pig, and the faculty of walking and standing was immediately, though slightly, implicated. The middle portions having been removed, the motions of the animal became tottering, and without order, as in drunkenness; the feet were moved rapidly and awkwardly; the animal tripped over its own limbs, fell, and then made inappropriate efforts to raise itself again, &c. The deepest portions of all being removed, the feet were often moved as if it would walk or run, but without stirring from the place. If the creature succeeded in standing up at one moment, it almost immediately fell down again, and so on. In another guinea-pig, Flourens removed the whole of the cerebellum at once, upon which all power to walk or stand was lost, although powerful efforts with the limbs were still made. Hertwig removed more than half the cerebellum in a cat: the motions, particularly of the fore feet, became irregular, the animal tottered, and fell forwards; if it was threatened, it endeavoured to fly, raised itself from the ground, but immediately fell again upon the side, or made a few steps back instead of forwards. The animal lived to the 9th day, the motions becoming continually more and more affected. Magendie's experiments of the same kind were followed by like effects; rabbits in their endeavours to escape, moved backwards. Budge removed at a single stroke the whole left half of the cerebellum, immediately afterwards the animal spun several times violently round to the left side; the movements were then less vigorous, but they were still all directed to the left. When at length all motion ceased, the creature sat upon the ground, still inclined to the left side. Upon the application of any kind of stimulus, the old spinning motion was resumed. Other similar experiments were always attended by the same effects. Hertwig and Budge observed great general muscular debility to follow wounds of the cerebellum, which was usually greatest immediately after the operation; when the shock of this had passed, the strength often returned in a certain degree. In the cases of disease of the cerebellum, and particularly in the one of original deficiency of the part observed and described by M. Combette (*Revue Medicale*, Avril, 1831,) Magendie, and Cruveilhier (*Anat. Pathologique*, Liv., 15, Pl. v.), there was great muscular debility in the extremities. [The subject of this celebrated case was a girl who died in her eleventh year; she was generally feeble, but she spoke, although with hesitation, and her legs though weak sufficed her to walk withal, and then, she used

consequently led to the conclusion that the office of the cerebellum was to co-ordinate or duly combine the voluntary motions—to regulate the harmony of motions in space[806]. Consciousness, will, and sensation still exist after injury to or removal of the cerebellum. The cerebellum would not seem to act as a reflector; injury of its substance is never followed by convulsions[807]. The effects of injury to the cerebellum appear above the decussation, that is to say, upon the side opposite to the one which has been injured. The cerebellum has been regarded as the central organ of the sexual appetite, but upon no sufficient data[808].

§ 362. Experiments on animals confirm the obvious anatomical connection of the meso-cerebrum (§ 346) with the organ of vision. Injuries of the corpora quadrigemina are followed by blindness on the side opposite to that on which the injury is done; the same consequence follows the partial or complete destruction of the thalamus. Injuries of these parts have precisely the same effects as direct inju-

her hands. The poor child was almost an idiot; *but as she spoke, and walked, and made use of her hands*, it is obvious that the cerebellum could have had nothing to do with the highly complicated movements requisite in all these acts. R. W.]

806 Budge calls the cerebellum an organ for the control of irregular or unbridled muscular power.

807 This, from the concordant results of different experiments, particularly those of Hertwig.

808 Gall was the author of this theory, and he has been followed by all late craniologists or phrenologists. Precise facts, however, have not confirmed, and pathological data seem rather opposed than favourable to his views. [Baron Larrey was nevertheless led by his extensive experience to conclude that "the cerebellum exerted a strongly marked vital influence on the genital organs." *Clinique Chirurgicale*, tom. 1, p. 297, 1829. "A young soldier of 18, received a blow upon the nape of the neck. He became alarmingly ill in consequence, and only quitted the hospital after three months' sojourn there. Fourteen years afterwards this man presented himself for discharge. He was thin, pale, and beardless, and his voice was piping and feminine. His genital organs were reduced to the size of those of a child a few months old;—the testes were not larger than small haricot beans. He stated that since his accident he had been without any sexual desire, although he had formerly been like the rest of his comrades in this respect, and that his beard, which was well grown at the age of 18, had since fallen out. His intellectual faculties had never been affected." *Ib.*, p. 303. "An artillery-man received a musket shot in the neck, the ball traversing the nape and grazing the occipital protuberances. The sight and hearing were much affected; the testes fell into a state of atrophy, and the penis shrunk in the same degree, and was altogether inactive." *Ib.*, p. 305. R. W.]

ries of the optic nerves themselves. Superficial injuries of the corpora quradrigemina do not destroy the contractile power of the iris, —the pupil continues moveable; but extensive injury or entire ablation of the parts paralyses the iris. Consciousness and memory are not destroyed by injuries done to the corpora quadrigemina. According to some observers, convulsions (on the opposite side) follow injuries of the corpora quadrigemina; according to others, nothing of the kind ensues. Muscular weakness, vertigo, and a disposition to turn to the side injured have been frequently observed. Increased movements of the intestines have also been observed when the corpora quadrigemina have been irritated[809].

§ 363. The primitive fibres which go to the constitution of the cerebral hemispheres have least of all to do with the simple motory and sensitive operations of the nervous substance. All inquirers agree in considering the hemispheres as altogether insensible; they may be cut and partially removed without any feeling of pain being excited[810]. But the senses of sight and smell are lost. The iris retains its contractile power. It is doubtful whether or not the sense of hearing ceases when the hemispheres are removed[811]. The obvious effects of such an operation are manifested on the side opposite to that which is injured. Muscular debility follows on one side, or in case both the hemispheres are excised on both sides; but, as it seems merely from the shock of the operation; the power of balancing the body and the strength are recovered after a short time. Some animals, birds and amphibia especially, will live for weeks and even months after extirpation of the hemispheres; but they

[809] The experiments of Flourens and Hertwig differ in some particulars. The former observed convulsions to follow injuries of the corpora quadrigemina, the latter did not. Hertwig asserts, that the sight is at first lost when these bodies are partially destroyed, but is by and by recovered. Flourens, Magendie, and Desmoulins, observed vertigo and lateral whirling. Budge (l. c., p. 152) is the author of the statement in regard to the small intestines. With reference to the motory fibres here alluded to, see later, § 364.

[810] On this subject, we have numerous experiments by Flourens, Hertwig, and Budge, and these are very readily repeated on frogs, and on birds—particularly pigeons and ducks.

[811] Flourens states that the hearing is lost when the hemispheres are removed; Magendie and Malcorps, on the contrary, found that it was not affected. The fact involved here, is of interest, because of the intimate anatomical connection of the auditory apparatus with the fourth ventricle and medulla oblongata.

require to be fed by hand[812]. Convulsions are not induced by removal of the hemispheres.

As the cerebral hemispheres consist in principal part of medullary masses, composed of very delicate primitive fibres, and a smaller admixture of gray matter or ganglionic corpuscles, the fibres appear to be of a peculiar kind, and are certainly not destined to act as conductors of sensation and motion. The hemispheres rather appear to be the exclusive instruments of the higher psychological activities. The anatomical relations already detailed, vouch for this fact, viz: the scanty development of these masses in the lowest grades of vertebrate animals, their imperfect formation in cases of idiotcy, their progressively larger size as the faculties increase in num-

[812] Quadrupeds are not nearly such good subjects for this experiment as birds, by reason of the great extent of wound that must be made, the copiousness of the hæmorrhage, &c. Instead of referring to several experiments in a general way, I shall here quote one at length, which Malcorps, of Lyons, performed, and which he describes particularly in a letter to Magendie (vide Magendie, *Maladies du Système Nerveux)*. The subject of the experiment in this case, was a pigeon, from which the cerebral lobes were removed on the 28th of April, 1839, and which was still alive and vigorous on the 8th of July, the date of the letter. The cranium was first removed, and the hemispheres taken away one after the other, with the handle of the scalpel. The wound was dressed with lint dipped in cold water to stop the bleeding. Four hours afterwards, the lint was dispensed with, and the flaps of the wound approximated, but not maintained by any kind of bandage. Next day, the creature was found not to take the food which was placed before it; the food was, therefore, put into its mouth, and the root of the tongue being touched, motions of deglutition were immediately induced, (reflex motions; vide § 358). At the time the letter was written, this pigeon was perfectly well in health, and had not even lost flesh. It required to be fed three times a day; it was only necessary to put the food into the bill; deglutition ensued forthwith. The fæces were normal; the motions of all kinds were free and unimpeded, the flight was only not so powerful as natural. Thrown into the air, the creature soon came down again of itself; it never flew more than about a couple of feet high. The general sensibility was normal; it was difficult to decide on the state of the sense of vision. When an object was thrust quickly before the creature, it did not move. When a light was approached, the pupil contracted, but the bird remained indifferent, and did not seek to escape. Confined in a darkened, or partially illuminated place, it was found, however, to seek out the light parts; and it avoided bodies that lay in its way. Strong odours did not appear to affect it; and sudden noises made no impression. At night it slept with closed eyes; but on the slightest noise it raised its head in a remarkable manner and opened its eyes, which anon it closed again. Its principal occupation was to prune its feathers and to scratch itself.

ber and in power, and their ample dimensions in eminently intellectual and moral men[813].

§ 364. Animals whose cerebral hemispheres have been removed, are dull in their senses, apathic, and only capable of manifesting reflex movements. They seem to be plunged in a sort of sopor, like men who are suffering under compression of the brain from the effusion of blood or of serum within the skull, from depression of a portion of the cranium, etc. The organic functions are performed for a certain indefinite time, and all, or the greater number, of the motions can be executed, but they no longer take place under the guidance of internal or mental behests. With regard to the functions of the several parts of the cerebrum, we have little more than hypothesis[814]. The commissures appear to secure unity in the operations. Injury of the corpus callosum and neighbouring parts, does not seem to occasion blunting of any of the powers—the senses remain active; and the sensibility to pain is undisturbed; several phenomena seem to accord with those that appear when the cerebellum is injured, so that the corpus callosum, like the cerebellum, has probably some connection with the voluntary motions[815].

813 [Reil expresses himself thus, in connection with this subject: "The brain is the organ of the internal senses [moral and intellectual faculties]. The nerves of the external senses and voluntary muscles, escape from the cranium forwards, and backwards, and ramify over the whole of the body in order to connect it with the organ of the soul; the nerves of the internal senses, again, have no object beyond the cranium, and are, therefore, found rolled up on themselves and forming the masses of the brain *(rollen sich in sich zur Masse des Gehirns zusammen.)* *Archiv für Physiologie*, 1802, B. vi. S. 406. Let us trust that if this be so, physiologists will speedily turn their attention to the discovery of these "nerves of the internal senses," and not leave by far the most interesting page in the history of their science the mere blank which it is at this moment. Diversity of apparatus in connection with diversity of function, appears to be one of the most invariable laws of the animal economy; and if mind be not one and indivisible,—if the several dissimilar moral and intellectual manifestations which we see in the world be not mere modifications of one power, but are rather distinct and different faculties of the soul, we may be as certain that each of them has its own special means of manifestation, as we are that smell, sight, hearing, taste and touch have theirs. Vide my quotation from Valentin, Annot. 766. R. W.]

814 Among the mere hypotheses, I place the older notions in regard to the function of the pineal gland, the pituitary gland, &c.

815 See Valentin's account of his experiments on the *corpus callosum*, in his *Repertorium* for 1841, p. 358. Symptoms of irregularity and of rotation in the

§ 365. The influence of the central parts of the nervous system upon the automatic motions is remarkable. The action of the heart appears to be influenced in the greatest degree by irritation of the anterior aspect of the upper part of the spinal chord and medulla oblongata; but some experiments seem to assure us that the motory nervous fibres of the heart also extend into the cerebrum[816]. Motions of the stomach were observed along with irritation of the cerebellum, corpora quadrigemina, thalami, and corpora striata. On irritating the anterior columns of the spinal chord through their whole extent, the medulla oblongata, the hemispheres of the cerebellum, the corpora quadrigemina, the thalami, and corpora striata, peristaltic motions of the small, and also of the great, intestines have been observed to take place. Powerful contractions of the rectum also ensued upon excitement of the parts above mentioned, and of the posterior portions of the cerebral hemispheres.

movements occurred when the part was injured beyond the middle line, but not regularly, and never with any force.

[816] On this and the following facts see Budge, l. c., and the observations of Valentin on his conclusions in the *Repertorium* for 1841, p. 325. Budge infers that the motory fibres of the heart terminate in the anterior part of the medulla oblongata, before the arresting fibres of the cerebellum cross or influence them. But Valentin, from repeated experiments, found that mechanical irritation of the medullary mass of the anterior lobe of the cerebrum, above the centrum ovale Vieussenii, and of the anterior part of the lateral ventricle, occasioned contractions of the heart generally, but particularly of the auricles. [These and other statements in the last paragraph ought to satisfy us that there is no necessity to suppose that any motory fibres of the heart, stomach, and bowels, extend to the corpora quadrigemina, thalami, and corpora striata. Every integral part of the nervous system is affected, through affections of any one part. The hemispheres, it is said, may be removed without the motory power being affected; but the sentiment of fear,—the causes for which are solely apprehended through the hemispheres—unhinges the whole muscular system, so that the limbs totter and refuse their office; ill news which we receive through the ear or the eye indifferently, make the heart to suspend its action, and the cheek to blanch; certain odours make us faint, &c. Motion is a very important faculty, certainly; but it seems absurd to be looking for its immediate instruments everywhere. Another conclusion that forces itself upon us in reading these accounts of mutilations of the brain is this: that they are incompetent to lead to a single safe and satisfactory physiological inference; or if any exception must be made, it is in connection with the functions of the anterior and posterior roots of the spinal nerves. R. W.]

The urinary bladder contracted when the cerebellum, and particularly the crura cerebelli, the valvula Vieussenii, and the corpora quadrigemina, are irritated. The influence of the central parts upon the motions of the genital organs is also remarkable. Irritation of the left hemisphere of the cerebellum and processus vermiformis, induces motion in the right vas deferens, testis, Fallopian tube, and half of the uterus, and vice versa[817]. From these experiments it appears that the automatic motions of the organs just named are as dependent on the brain and spinal chord as are the muscles of animal life, and that the primitive fibres of the sympathetic nerve, passing through the spinal chord and pons, are in connection with the brain, and particularly its base. Some portion of the motory fibres of the intestines, however, must reach the crura cerebri,—they do not all enter the cerebellum. In this way is the influence of the central parts upon the organic functions, as well as the reciprocal reflex actions of both in connexion with mental emotions, explicable.

§ 366. It would appear that the presence of the cerebro-spinal fluid in due quantity was quite essential to the due performance of their functions by the brain and spinal chord. This fluid is met with both in warm and cold blooded animals. Underneath the bony coverings, betwixt the pia mater and tunica arachnoidea, the whole of the spinal chord, nervous roots included, is literally surrounded by this fluid ; farther, it covers the surface of the hemispheres, and collects particularly in all the depressions and inequalities, an arrangement by which the brain, cerebellum, and medulla oblongata, are all alike kept slightly apart from their bony coverings, and the effects of shocks upon the delicate nervous centres are lessened, at all events. The cerebro-spinal fluid can be drawn off in animals ; to the operation succeed muscular debility, and blunting of all the senses ; which are only of temporary continuance, however, for they disappear with the reproduction of the fluid which takes place very rapidly[818].

[817] Valentin says that young animals must not be taken for this experiment. When the subjects are sexually mature, or are in heat at the time, the vasa deferentia and Fallopian tubes exhibit very powerful peristaltic motions. During and after intercourse, similar movements take place as reflexions (§ 37 and 38.)

[818] Magendie has directed the particular attention of physiologists to this fluid [which he has thought worthy of consideration, in a respectable sized 4to,

General Remarks on the Functions of the Great Nervous Centres.

§ 367. The great centres of the nervous system unite or combine the functions performed by its various and dissimilar parts into an harmonious whole. From them are sent forth by the channel of the centrifugal fibres the behests of the will in reference to voluntary motions, and they are no less necessary, as we have seen, to the performance of reflected movements, the stimuli to which attain the centres by the route of the incedent or centripetal fibres. It is in the central parts and even exclusively in the hemispheres, as it would seem, that consciousness of impressions is attained. The feelings of pleasure and pain, in alternations of which our whole life is passed, only exist along with integrity of the hemispheres. The nerves in their centripetal organs of sensation are mere conductors of external impressions. The most important conductors, which make us acquainted with the existence and properties of the external universe, are the nerves of the senses, which have consequently particular parts of the brain in connection with them. These parts are situated towards the middle line of the base of the brain especially, and are covered by the commissures and hemispheres, with which they stand in the most intimate anatomical and physiological relationship. The organic vital processes are also, although it may be somewhat more remotely, under the dominion of the central nervous masses, as we have already seen, so that the soul stands in a more or less intimate relationship to the entire phenomena of the somatic life. The integrity of the psychological phenomena, again, is essentially dependent on an harmonious combination of the whole of the physical vital processes. The more

volume, illustrated with plates: *Considerations on the cephalo-rachidian fluid*, &c., Paris, 1843. R. W.] This fluid in question is not wanting in man; I have found it in large quantity, especially in the bodies of persons who had died suddenly. It is very easy to procure it from the living animal; the muscles at the back of the neck are divided, and a puncture is made between the atlas and occiput through the connecting ligament and investing membranes; it often springs out in a stream. The disturbance which follows the abstraction of the fluid may readily be referred, as Valentin has done, to the change in the physical state—diminished pressure upon the nervous centres—which must immediately ensue.

particular consideration of these, and the study of the disturbances they suffer from disease, are evidently within the scope of the general and applied physiology, which it is our purpose to discuss particularly, in a separate Book.

SECTION IV.

OF MOTION.

Preliminary Observations.

§ 368. The peculiar motions of the matter which constitutes organic bodies are distinguished from external physical motions by this, that they only occur as phenomena accompanying life. Some of these phenomena of motion are not only most intimately associated with the nervous system, but also with the soul; for by an act of the will we can call them into play. To this category belong the VOLUNTARY MOTIONS. Wherever we see these motions occurring, we encounter a particular tissue as their immediate agent, a tissue which is universally known under the name of MUSCULAR TISSUE, or flesh, the intimate structure and properties of which, are forthwith to occupy our particular attention; at the same time that we take occasion to consider a few of the most important combined muscular movements. The motions which are characterized as INVOLUNTARY or AUTOMATIC, are also in major part effected by means of muscular tissue; but the tissue of involuntary muscles differs histologically from that of voluntary muscles. The muscular tissue also passes by inappreciable degrees into other forms of contractile fibrous tissue, so that it is difficult to define its limits precisely. Other motions of a peculiar kind, and independent to all appearance of the muscular or contractile system, have lately been discovered, and are now generally spoken of under the title of CILIARY MOTIONS. These motions seem farther to be abstracted for the most part from the direct influence of the nervous system, which, although remotely, is still manifestly enough in connection with the

involuntary muscular movements. There are other motory phenomena which occur in the very lowest grades of animal life especially and may be assimilated to the ciliary motions. These movements we can only allude to in this place, from their being rather subjects pertaining to the General Physiology, which embraces the consideration of the primary phenomena of motion and the laws of organic nature at large.

CHAPTER I.

OF MUSCULAR MOTION IN GENERAL.

Structure of Muscles.

§ 369. The muscular tissue is distinguished from all the other contractile tissues, although there be no very definite line of demarcation between it and them[819]. It is for the most part of a red, reddish-brown, yellowish, or white colour; the shade in any case being due to the tint, and greater or less abundance of a peculiar pigmentary matter, which enters into its constitution[820]. It is

[819] We have a great many microscopical researches into the muscular tissue. It was very long, however, before observers could agree upon a very few particular points; and even at the present time, almost all that can be said is, that we all admit a certain class of muscles, the constituent fibres of which are streaked across, and another class, the fibres of which are continuous, and marked by no kind of striæ. With reference to the arrangement of the ultimate elements, some difference of opinion still prevails, and we cannot allow ourselves to consider the accounts we have of the appearances observed as otherwise than hypothetical. Weber's Hildebrandt contains the older literature upon this subject. Henle in his Söemmerring is very full on the matter, as is Mandl also, *Anat. Miscropique*, 1*ière livraison*, 1838. Among the latest researches, are those of Skey, *Philos. Trans.*, 1837, of Bowman particularly, (*Ib.* 1840,) and of Henle, (*Söemmer.*, p. 573). The histological elementary works of Bruns, Krause, Gerber, and to conclude, the article MUSCLE, by Valentin, in the *Berlin Encyclop. of Medical Science*, vol. 24, p. 203, contain all that is known on the subject.

[820] In man, and the greater number of the vertebrata, the muscles are red; the majority of the bony fishes, however, have white or yellow flesh; in a few, nevertheless, the flesh is of a pretty deep red, as in the tunny.

soft, and for the most part easily torn. It is very obviously made up of bundles of fibre, which show a kind of special sensibility to the galvanic stimulus. When boiled, muscular fibre does not undergo any very remarkable change, it yields but little gelatine to boiling water[821].

§ 370. Taking the first and most obvious microscopical characters as our guide, true muscular fibres may be divided into two principal kinds or varieties. 1*st*, Simple unstreaked or organic muscular fibre; and, 2*d*, Compound, streaked, or animal muscular fibre.

The first kind, or muscular tissue of organic life, consists of smooth, cylindrical, and generally pale coloured fibres, arranged parallel to one another, and forming bundles, which are connected by means of cellular tissue, but are still of great delicacy, most easily lacerable, and appear to be without sheaths. This kind of muscular fibre is principally met with in the internal hollow parts of the body, as in the stomach, intestines, and bladder, where they are highly developed. The fibres observed in the excretory ducts of the larger glands, the gall ducts for instance, those that enter into the constitution of the parietes of the veins, and that are found in the septa of the penis [scrotum], and clitoris, also appear to belong to the same genus[822]. The finest or ultimate fibres of the muscles of organic life, measure about the $\frac{1}{1000}$th of a line in diameter; they

[821] We are in some sort obliged at this time to include these physiological and chemical characters, in the definition of true muscular tissue. [Dr. John Davy has many highly interesting observations on the action of boiling water, and of long boiling on the textures of the human body, which require a particular reference like everything else which this distinguished physiologist has touched. Vide his *Researches Anatomical and Physiological*, vol. ii, p. 313. R. W.]

[822] Among the voluntary muscles, cross-streaking seems to fail only in the retractors of the penis and clitoris, and constrictors of the vagina, [muscles, which, if they obey the will at one time, seem also to act independently of it at another. Mr. Gulliver sometimes found fibres of the voluntary muscles entirely without transverse streaks. In the pectoral muscle of the long-eared bat, (Plecotus auritus,) for instance, most of the fibres were observed to be simply very minutely and irregularly granular, and quite destitute of transverse streaks. See Gerber's *Anatomy*, Note, p. 235. This observation would seem to support the opinion of Wagner, (Note, p. 648,) that the striated appearance is rather connected with a contracted state of the fibres, than with the arrangement of the beads or discs of which the finest or ultimate fibres are said to be composed. R. W.]

are always isolated with much difficulty, and are not susceptible of farther analysis by the microscope.

2*d*, Compound or streaked muscular fibres. These form the great mass of the muscular system. They are more especially distinguished by the red colour which so commonly belongs to muscular flesh, and occur almost without exception in voluntary muscles,—those of the eye, internal ear, tongue, velum palati, greater part of the œsophagus, diaphragm, and sphincters, all belong to the streaked class. The muscular fibres of the heart, however, are also cross-streaked, in spite of the distinguished position of the organ in the system of organic life; the striæ are fainter here, indeed, than in the ordinary voluntary muscles, but they are still decided enough.

Cross-streaked muscular fibres are by no means confined to the higher vertebrata, they occur in many members of the invertebrate series, such as insects and crabs, and in others still lower in the scale than these[823]. In various animals, again, possessing very decided powers of voluntary motion, nothing but simple unstreaked muscular fibres are encountered. It may be said generally, that the cross-streaked muscular fibres pertain to the system of animal life, the simple or unstreaked, to that of organic or vegetative life; that the former are developed from the serous, the latter from the mucous lamina of the germinal membrane.

§ 371. Observers are by no means agreed as to the morphological cause of the cross-streaking of the voluntary muscular fibre; it is, indeed, extremely difficult to give a decided opinion upon the subject; there is, in fact, another point involved in the conclusion come to, viz. whether the primitive muscular fibres are simple, and even, and delicate filaments, or consist of moniliform or bead-like series of discs or globules. Upon this subject we have two predominating views. According to one of these, primitive muscular fibres consist of moniliform bands, and the cross-streaking is nothing more than the optical expression of this histological fact—the successive rows of discs lying parallel to one another, give the appear-

[823] They are very beautifully seen in insects. I have lately observed them in the medusæ (*Icon. Zootom.*, Tab. xxxiii). Eschricht saw them in Salpa, so that delicacy of organization, and even transparency of substance, is no hinderance to their development. Worms, snails, and polypes appear to possess simple unstriated muscles only. See my paper in Müller's *Archiv*, f. 1835.

ance of transvere striæ. According to the second class of observers, the primitive fibres of the cross-streaked muscles are as smooth and continuous in themselves, as those of the muscles of the organic life; the transverse marking they conceive is due to the presence of a delicate transversely wrinkled sheath which unites the primitive fibres into fasciculi; in the opinion of other observers the sheath is wrapped spirally around the bundles, and can even be unwound from them[824].

§ 372. The following points can be made out with tolerable certainty in the microscopical examination of the transversely streaked muscular fibre, which may be assumed as the tissue in its highest state of development. The muscular fasciculi of the anatomist, the larger bundles, manifest to the naked eye and separated from one another by distinct sheaths of cellular substance, are readily separable into a series of finer and finer fasciculi, which are spoken of as the muscular fibres. These fibres are from $\frac{1}{30}$th to $\frac{1}{100}$th of a line in diameter, of a prismatic shape, three, four, and five sided, and of very various length in different muscles, for they appear generally to run through the whole of the muscle from its origin to its insertion, without undergoing division or suffering interruption.

[824] Schwann and Müller are the principal advocates for the first of the views above detailed; for the second, Lauth, Jordan, Krause, Bruns, and others, and at a former period, Valentin and myself. Henle is doubtful, as are also Valentin and I at this time, without, however, participating in the opinion of Schwann and Müller. Mandl admits a scarcely perceptible spiral band, similar to the spiral filament of the tracheæ of insects. For the rest, Valentin, Henle, and I, throwing the question of the sheath aside, do not admit the transverse streaking as the optical expression of a moniliform structure of the primitive fibres; it rather appears to us to be due to a notching of the primitive fibres in a state of partial contraction. [Dr. Martin Barry is the last English writer on the muscular fibre (*Phil. Trans.*, 1841). He regards the ultimate or finest fibre as a spiral, so arranged in the fascicle as to produce the transversely streaked appearance. Bowman, (*Phil. Trans.* 1840,) agrees with Schwann and Müller in considering the transverse striæ as due to the arrangement of the discs or granules of which they describe the ultimate filament to be made up. The views of Barry and Bowman, therefore, as to the structure of this filament, are as opposite as possible, and not to be reconciled; while the fact observed by Gulliver, that the muscular fibres of adult animals are often destitute of transverse streaks, is not at all explicable by either of the foregoing opinions, but rather leans to that of Wagner, who supposes the notched appearance of the fibres to be due to a partially contracted state of them. R. W.]

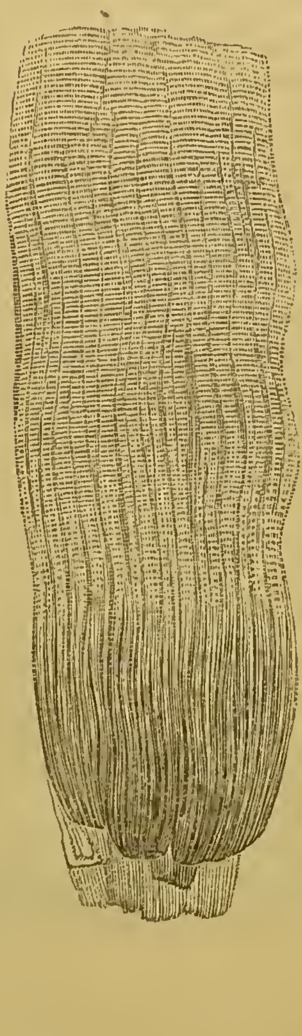
A variable number of the fibres now described, go to constitute the muscular fasciculi; but they are by no means the ultimate elements or fibres into which the muscular substance can be separated. When a small portion of a fresh muscular fibre from the body of man or an animal is viewed with a power of from 200 to 300 linear, the focus being delicately adjusted to the superficies of the specimen, delicate, somewhat sinuous, transverse striæ which extend completely across the fibre, come into view. These striæ run parallel to, and at the distance of from the $\frac{1}{800}$th to the $\frac{1}{1000}$th of a line from one another; they bear a certain resemblance to the lines on the volar aspect of the extremities of the fingers[825]. If the surface only of a muscular fibre be examined by an aplanatic eye-piece, without, at the same time, penetrating more deeply, nothing but transverse striæ are perceived; but if the focus of the microscope be set somewhat lower than the surface, then divisions in the length of the fibre, as well as across it, present themselves, and the more deeply the eye penetrates, the more distinctly do these longitudinal parallel striæ,—the optical expression of the primitive fibrils, come into view, whilst the transverse striæ disappear. Primary or ultimate muscular fibres may be exhibited isolatedly, by means of slight maceration and teasing out with needles. They are excessively delicate filaments, no more than $\frac{1}{1000}$th of a line in diameter, pretty even in their surface, and not properly articulated. [The moniliform appearance of single muscular fibrils, however, has generally presented itself to me very distinctly of late: as the instrument is coming into focus, the fibril presents itself literally as a string of delicate rounded beads, distinct from one another; the

825 [According to Bowman and Gulliver, the size of the fibres differs considerably in different muscles and in different animals, and even in the same animal at different periods of existence. The size of the transverse streaks, or of the distance between them, is likewise so variable, that Gulliver particularly mentions fine and coarse transverse markings, mostly distinct in magnitude, and not running by imperceptible gradations into each other. These two kinds of marking sometimes occur in the same muscle, but more frequently in different muscles of the same animal. In the common swift (Hirundo apus), for example, the transverse streaks were observed to be coarser and plainer in the muscles of the leg than in the pectoral muscles, a curious fact, when the relative exercise of the wing and leg of this bird is considered. The most extensive series of measurements which we possess of the fibres of different muscles, and of these fibres in different classes of animals, are given by Gulliver.—See *Proceedings of the Zoological Society*, Sept. 1839. R. W.]

focus is obtained, and it is a pretty even thread, but still obviously made up of darker and lighter portions; the focus is passed, and it is again resolved into a string of delicate cornelian beads. R. W.] The presence of any sheath the wrinkling of which might produce the appearance of streaking, the cavity described by some writers as occupying the middle of the muscular fibres, around which the primitive fibrils are supposed to be arranged, the actual form of the primitive fibrils, and so forth, are all so many points which at the present time are subjects of speculation, and not susceptible of demonstration[826].

[826] I have here been purposely extremely guarded in my expressions, and described no more than can be demonstrated to and seen by every one. The more we examine, the more difficult do we perceive it to be to speak decidedly in regard to the ultimate or elementary parts of the tissues. I shall here, in the freedom which the note allows me, pursue the controverted subject of the elementary structure of muscular tissue a little further than I have done in the text. In fig. CCXXXI. we have a fresh muscular fasciculus of the ox, $\frac{1}{30}$th of a line in thickness, represented as it is described above, and as it may be seen by every tyro in the art of microscopical observation. The upper extremity of the bundle exhibits transverse striæ only; but they appear to fail here and there, and these gaps seem as if they separated fibrils or bundles of fibres at some little distance from one another; the opposite or lower end of the fasciculus, on the contrary, shows nothing but longitudinal striæ or primitive fibrils, an effect which is entirely due to the focussing of the microscope. At the place where the muscular bundle is torn through (inferiorly) a scaliform appearance is perceived very beautifully brought out by the different layers of the primitive fibrils, which have contracted again in different degrees after yielding to the tearing force; in the middle of the specimen the microscope is so focussed that transverse and longitudinal striæ are perceived at the same time; here the former, there the latter, more distinctly, according to the difference of level of the surface of the fibre examined. The transverse striæ are in a general way extremely constant, and a highly characteristic indication of the muscular fibre of animal life, so that the smallest portion of a muscle belonging to this system is at once recognized under the microscope by their presence. The transverse striæ, however, become ex-

Fig. CCXXXI.



Vital Endowments of the Muscular Tissue.

§ 372. All muscular tissue, the cross-streaked as well as that which is without transverse markings, possesses the remarkable property of shortening under the influence of internal or external

tremely faint under many circumstances; in bodies with very soft or flabby muscles, and in very young animals, for example; but even here they are often very distinct, and are readily studied in the living larva of the frog, near to the spinal column in the tail. They are very distinct in boiled and roasted meat, and in muscle that has been macerated in spirit, (Fig. CCXXXII, CCXXXIII, B.) in which, indeed, they often present themselves as abso-

Fig. CCXXXII.

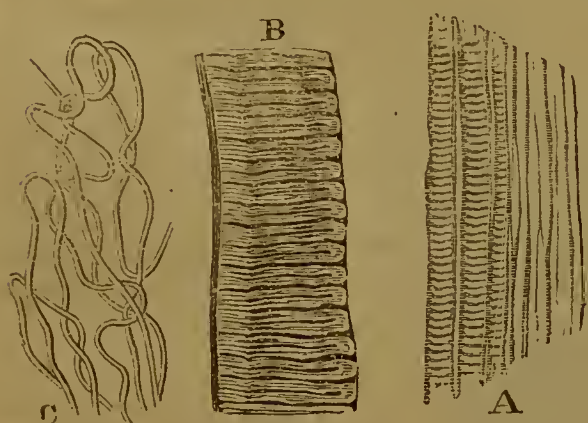


Fig. CCXXXII. — Structure of human muscle; a portion of the attollens auriculæ, which had been long kept in spirit. A, A number of primary muscular fasciculi, magnified about 200 diameters. B, A single fasciculus more highly magnified. C, Some fibres of cellular tissue interposed between the muscular fasciculi.

Fig. CCXXXIII.

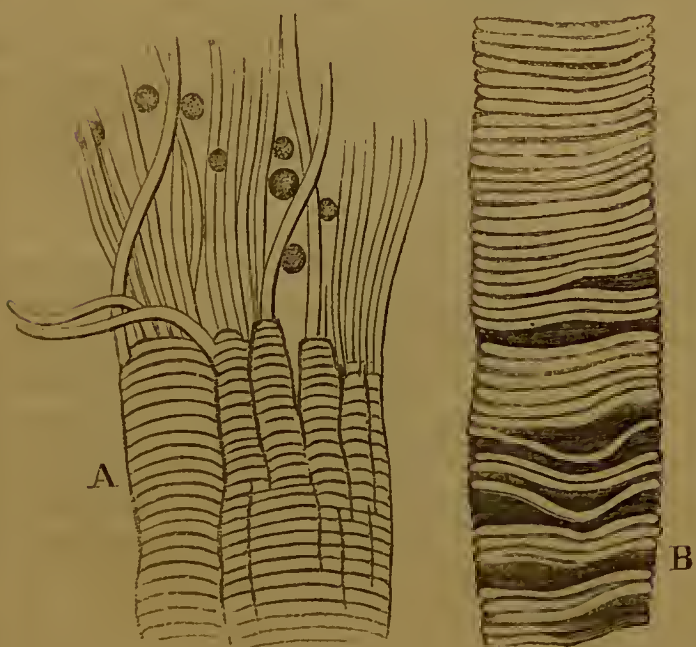


Fig. CCXXXIII.—Muscular fibre, after Skey. (*Philos. Trans.*, 1837.) A, Fibra Muscularis—primitive muscular fasciculus. Superiorly the primitive fibres are separated from each other; the globules are blood-discs to serve as standards for the estimation of their diameter. B, A primitive muscular fibre, to show how the transverse striæ are produced, and that they may be severally seen as elevations.

stimuli. At one time it was presumed that this motility of the muscles depended on a peculiar inherent irritability, which was

lute transverse rugæ, with lateral notchings, so that we should be very apt to suppose that a peculiar sheath enveloped the muscular bundles, a supposition which gains strength from the fact, that towards the torn ends of the specimen, the primitive fibrils are often seen free, isolated, and without any appearance of cross-barring (Fig. CCXXXIII. A.) On the other hand, however, we frequently recognize the transverse streaking upon the several isolated primitive fibrils (Fig. CCXXXIV, A and B.) It would seem that transverse sections ought to supply the surest grounds for conclusions; but no such thing as a sheath can ever with certainty be shown in the circumference of the muscular fibres, however prepared by hardening, &c. [Very good views of transverse sections of muscular fibres are given by Bowman, who has also plainly and truly depicted the sheath, or sarcolemma, as he terms it, of the fibres. In fact, this sheath may often be

Fig. CCXXXIV.

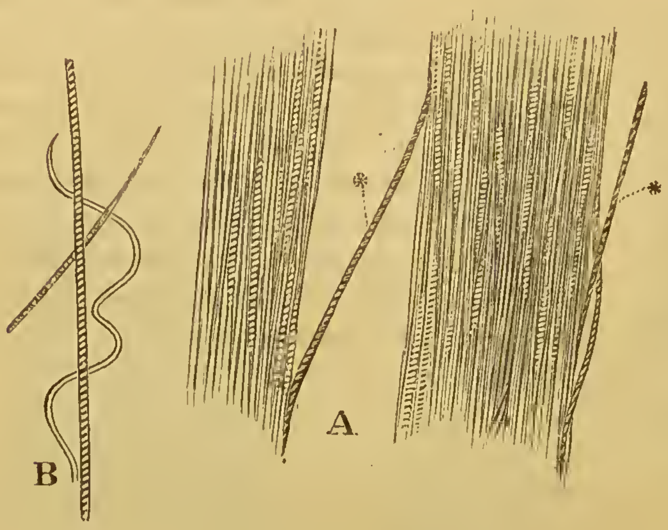


Fig. CCXXXIV.—Two primary muscular fasciculi from the dorsal muscles of a rattle-snake, which had been long kept in spirits. At * and * fine fibres are seen distinctly brought into view by separating the muscular bundles; they seem each to consist of several primary or ultimate fibres. B, Two of these fine filaments, seen under a power of 800, which exhibit crossmarkings. The sinuous filament is cellular tissue.

Fig. CCXXXV.

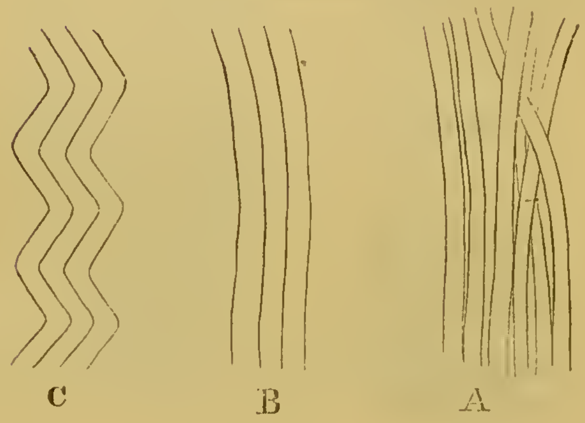


Fig. CCXXXV.—A, A bundle of fibres without cross striæ, from the muscle which closes the shell of Unio pictorum. B, A muscular bundle without cross-streaking from the Distoma duplicatum. C, The same bundle thrown into zig-zags at the moment of contraction.

designated MUSCULAR IRRITABILITY, and regarded as among the number of fundamental organic forces. But more recently that

seen with great distinctness in the perfectly fresh muscles of the lower vertebrate animals, in the eel, for instance. R.W.] Those observers, who, with Skey, Valentin, and others, admit a canal in the interior of the muscular fasciculi, arrive at this conclusion mainly from the examination of very recent muscular tissue, the bundles of which when cut across frequently spread out, or show a disposition to become everted, in their entire circumference, by which a kind of funnel-shaped aperture is produced. I have not, any more than Henle, been able to satisfy myself of the presence of any such canal in the muscular fibre of man and the vertebrata, although I will not say positively that it does not occur; and indeed, it is curious that I entertain no doubt of such a structure as that just mentioned being constantly present in the cross-streaked muscular fibres of the medusæ. See my paper on the structure of Pelagia noctiluca, 1841. The medullary matter which Henle found in the centre of the muscular fibres after treating them with acetic acid, I cannot help considering as due in part, at least, to the chemical agency of the acid. All artificial methods of preparation, such as maceration, the addition of reagents, &c., employed to bring out the moniliform structure of the primitive fibrils are objectionable; we dare not draw any positive inferences from the appearances presented after such treatment; indeed, the farther we advance in histology, we see ever the more clearly that the most important results are still obtained from observations made on parts in the freshest state possible, without the use of reagents of any kind, care being taken merely to separate tissues mechanically, and to fit them for inspection, by adding a little albumen ovi or serum sanguinis to them. Prochaska has given good representations of the coarser elements of the muscles,—the aggregation of the muscular fasciculi, &c.,—*De carne muscu-*

FIG. CCXXXVI.

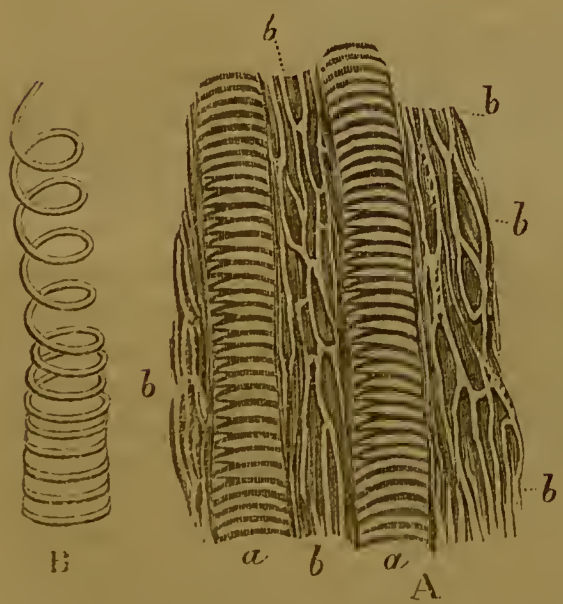


FIG. CCXXXVI.—Muscular fibre from the œsophagus, about three inches below the pharynx, to show the union of muscular fibres of the animal (*a*, *a*,) and of the organic (*b*, *b*) life, after Skey. B, Plan figure of the spiral fibre, which, according to some, surrounds the primary muscular fasciculi, and gives the appearance of cross-streaking. After Mandl, *Anat. Microscop.*

view has obtained very extensive accredance, according to which, the motory power of the muscles, or rather the occurrence of motion among their particles, on the application of a stimulus, is by no means peculiar to the muscles, but the capacity is entirely derived by them from the nerves. And, indeed, it plainly appears from experiment, that muscular contraction is immediately dependent on the nervous system; when the nerves which proceed to muscles are stimulated, contractions of these muscles are immediately induced (§ 237). It is true, indeed, that the direct application of a stimulus to a muscle is followed by the same phenomenon; but it would seem that this is only in consequence of the muscle containing nervous fibres. If any small parcel of muscular fibres be freed very completely from its nervous substance, it ceases to react on the application of stimuli. The most powerful stimulus in reference to the cross-streaked muscular fibre is the galvanic, and this is the one that is employed in preference to any other in the course of our experiments; but it is otherwise with regard to the muscular fibre of automatic life, upon which the direct application of mechanical

lari, Vienn. 1778. The intimate structure is excellently displayed, both by Bowman and Henle, as also in the accompanying figures. I particularly recommend the muscular elements of the dorsal vessel or heart of Scolopendra for the study of the natural resolution of the muscular fasciculi into fibres, and of their termination in elastic tissue. (Vide Fig. CCXXXVII.)

Fig. CCXXXVII.

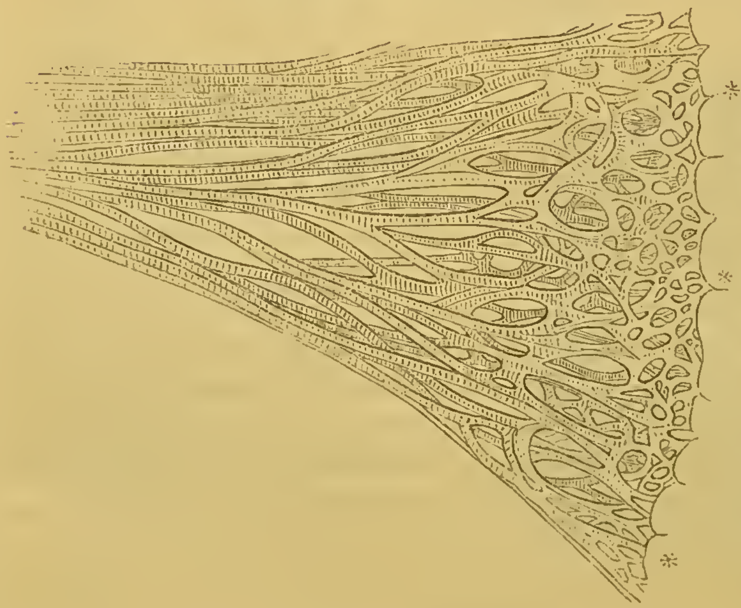


Fig. CCXXXVII.—A piece of a wing-shaped muscle from the Scolopendra Afra inserted at * * * into the dorsal vessel of the insect. The transition of the striated muscular fasciculi into a net of elastic tissue is very beautifully displayed.

and chemical stimuli appears to produce a more powerful effect than galvanism[827].

§ 373. Muscular contractions are either tonic, *i. e.* they continue for some considerable time, or they are clonic, *i. e.* they are rapidly succeeded by relaxations. Clonic contractions are frequently spoken of under the name of convulsions. These phenomena are most intimately connected with the state of the nervous system. Slight and passing stimulation, the direct action of stimuli upon the peripheral parts of the nervous system, for example, stimuli applied after separation of the nerves from the central parts, excite clonic contractions only, as may be seen in simple experiments with any kind of galvanic apparatus, (§ 243). These clonic contractions or muscular convulsions are by so much the more extensive and powerful, the stronger the galvanic stimulus is under the influence of which they are excited. Tonic spasms, such as we observe in tetanus, appear always to be effects of reflex actions,—at least they never occur save in connexion with the influence of the central parts of the nervous system. We can therefore excite tonic contractions by the agency of the will, and we have too frequently occasion to see them aroused under the influence of a peripheral stimulus acting upon the central parts,—as in traumatic tetanus.

§ 374. Many other phenomena exhibited by the muscular system

[827] The Hallerian doctrine of irritability has been very commonly abandoned in these times. Humboldt, Jo. Müller, Valentin, and others, have sought by experiments to show, that Haller's muscular irritability was nothing more than nervous irritability, and that the nerves themselves, when separated from the brain and spinal chord, soon lose their power of conducting stimuli to the muscles, and causing them to contract, (vide § 241). Stannius has very lately reasserted a proper irritability for the nerves—Froriep's *Notizen für* Sept., 1841. The criticism of these views belongs to the General Physiology. [It has always appeared to me a needless refinement in physiological views, to refuse proper irritability to the muscular fibre. Undoubtedly unless the muscular fibre form a part of the living organism, unless it be duly supplied with nerves, and with blood as well as nerves, and be maintained at a proper temperature, being duly supplied both by blood and nerves, it soon ceases to manifest any faculty of contraction; but surely the nerves are still only the medium by which the muscles receive the dictates of the will to contract or to remain at rest: the nerves convey the stimulus necessary to the excitement of contraction, but not the immediate contractile force which, upon every principle of sound physiology, must be held to belong to the muscular fibre itself,—or wherefore is it there? R. W.]

have also their primary cause in the nervous system. To this must probably be referred what we call muscular TONE, that state of tension of the muscles during life which is so different in different muscular parts, and under different circumstances. Tone is, in fact, but an inferior degree of contraction in the muscular system generally, independent of consciousness and of will, and only disappears with the extinction of life. The natural state of various muscular parts is even this tonic state,—the sphincters of the anus and bladder are always, save at the brief periods of defæcation and micturition, in a state of powerful contraction. The muscles have always a much higher tone during watching, than during sleep; and in circumstances of danger and difficulty, the whole muscular system is in a state of exaggerated tension. In the soundest sleep, however, the tone of the voluntary muscles is much greater than it becomes in many diseases,—the last stages of nervous fever, for example, in which patients seem literally to sink together in their beds. Paralysis of the muscles also depends on the nerves[828].

§ 375. The grouping and disposition of the muscles are most intimately connected with their functions, with the form and wants of the organism, and consequently with the nervous system at large. The muscular system of man and animals is so arranged, that one group of muscular fibres and entire muscles act as antago-

[828] Physiologists are not yet agreed as to the cause of the cadaveric rigidity; whether it is to be ascribed to an active contraction of the muscles, or to a change in the state of their constituent principles,—coagulation or condensation of their substance, &c. From the numerous observations of Sommer, *De signis mortem hominis absolutam indicantibus*, Havn., 1833, (Henle, *Op. Cit.*, p. 595), cadaveric rigidity appears never to occur sooner than sixty minutes, nor later than seven hours after death. Beyond all doubt, stagnation and change in the blood of the capillary vessels of the muscles must have some influence in the phenomenon in question. The intimate dependence of the muscles on the central nervous parts appears by the differences in their tone in syncope, in alarm, under the influence of spirituous liquors in different doses, &c. Painters and statuaries have long seen the necessity of attending to this circumstance in their works; the form and disposition of the trunk and extremities, the whole physiognomy of the body, is different in one asleep, drunk, and dead. [If paralysis of the muscles often depend on an affection of the nerves, still it does not so invariably; the supply of blood cut off from the muscles, the nerves being entire, is followed by paralysis; inflammation of the muscular substance is accompanied by paralysis, &c. R. W.]

nists to other groups and particular muscles, and maintain them is their state of equilibrium. Hence we have systems of flexors and extensors, of adductors and abductors, of sphincters and levators or relaxers, circular fibres and longitudinal fibres, etc. In the ordinary state, each system possesses a medium tone; or otherwise, one of them is somewhat superior to the other. In morbid states, spasms and contractions supervene, and these are apt to end in exhaustion and paralysis. Muscular movements in health always take place on one or both sides of the body, in suchwise that definite general motions, having specific ends, result, and this, whether the motion be voluntary or involuntary, whether it be performed with consciousness or without it. The same law obtains in regard to all instinctive movements; it holds good in reference to decapitated animals, to the motions of the embryo, etc.[829].

§ 376. The muscular substance itself is immediately concerned in all those actions which we shall comprise under the head of MECHANICS OF MUSCULAR MOTION, and shall treat of in detail, in the following Chapter. Here, the local effects of the muscles appear immediately connected with the direction in which the contraction of their fibres takes place, which in its turn is determined, and often greatly modified by the points of attachment of the muscle that is active, as also by the combined action of portions or of the entire masses of other muscles. Every individual muscle is in itself an active and entire organ, each of its several fasciculi, however, having its own functions. When we expose the large muscle of an animal, or when in such an operation as the extirpation of a mamma in the human subject, we have a broad muscle like the pectoralis major laid bare, we perceive the play of the particular muscular fasciculi, which seem to move in some sort like the keys of a piano-forte.

§ 377. The motions of the finest elements of the muscles is of peculiar importance, and only to be observed under the microscope. The best subjects for observation here, are small invertebrate animals, which may be brought either in major part, or wholly under the microscope[830]. Two principal acts seem to go on: 1*st*, Slight and

[829] See farther on these topics, the Third Section of this Book.

[830] Small crustaceans, and particularly the transparent larvæ of insects which are so generally to be found in stagnant ponds and ditches, are excellent

somewhat undulatory wrinklings pass over the whole of the muscular surface, at the same time that the fibrils appear to oscillate and to tremble. In the cross-streaked muscles, the transverse markings become more distinct at these times, and formal elevations and depressions, or projections and notchings are perceived[831]. *2d*, Larger or more decided bendings occur, in consequence of which, the muscular fibres and fasciculi acquire a zig-zag disposition, (Fig. CCXXXV, C,) and become distinctly shorter—they shorten from a fourth to a third of their entire length. These zig-zagings, which are more pronounced as the contraction of the muscle is more energetic, extend from the larger to the smaller fasciculi[832]. The precise mode in which the primitive fibrils stand affected under these circumstances, cannot be determined by direct observation. They seem always to partake in the zig-zag disposition of the coarser fasciculi; whether or not they contract to any greater extent, and of themselves, is unknown. We are certain of this much, however, that no change occurs in their substance—in the state of their molecular aggregation[833]. Experiments have satis-

subjects for observation. I have never seen the zig-zag markings more beautifully displayed than in the muscles of the tail of the distoma duplicatum, a suctory intestinal worm which lives as a parasite on the common fresh-water muscle (Anodonta), (Fig CCXXXV, B, C). The muscles here have no transverse striæ.

[831] By this we can also explain wherefore the cross streaking should be so beautifully seen in the muscles of animals that have been preserved in spirits, it may be for many years.

[832] I have observed these bendings so strongly marked, in distoma duplicatum, among other subjects, that the angles which are generally obtuse, here passed into absolutely right angles.

[833] Many accordant experiments force us to abandon the old notion of the muscles occupying less space in a state of contraction than in one of repose. Ermann, in particular, showed that the water sunk in a graduated tube to so inconsiderable an extent during the contraction of a muscle, that it could not be estimated. [My able friend, Mr. T. Wharton Jones, has lately given a new view of the cause and mechanism of muscular contraction. Assuming Mr. Bowman's conclusions on the structure of muscular fibre to be correct, viz. that it consists of a series of pieces in the form of discs, not, however, immediately adherent to each other, but held together by an intervening substance, so yielding and elastic as to admit of very close approximation of the discs to each other, or of their separation to a certain extent, he regards these discs as analogous in their nature to electro-magnets; and proposes to call them *neuro-magnets*,

fied us that the muscular power is inversely as the degree of contraction. Every muscle has its greatest power in its normal length; at the extent of its contraction its force is reduced to zero[834]. In repose, the fasciculi and primitive fibres resume their straight

inasmuch as the relation of the nervous influence to them appears to be essentially the same as that of the galvanic influence to the soft iron forming common electro-magnets. The neuro-magnetic discs, then, composing muscular fibre, of microscopical minuteness, are arranged so as to operate on each other at very short distances only, and therefore with great power—a power which, as in other cases of attraction, goes on to augment in a rapidly increasing ratio, as the discs approach each other. By the multiplication of the neuro-magnets in the linear series constituting a muscular fibre, due though limited extent of motion is obtained; and according to the number of linear series arranged side by side in a muscle, so is the power of that muscle. The primitive fibrils of the nerves are disposed in loops across the muscular fibres, not coiled round the neuro-magnets as the conducting wire is around electro-magnets when much electro-magnetic force is required. But this is not a difference in principle, it is merely one of arrangement; the nervous influence streaming along the primitive fibrils of the nerves, thus disposed in loops across the muscular fibres, communicates to the neuro-magnetic discs composing these fibres, a magnetic state in the same way that the galvanism conducted by the wires of electro-magnets does to the soft iron of which these magnets are composed; by virtue of the magnetic state which the neuro-magnetic discs of muscular fibre thus acquire—some directly, some by induction—they attract each other: and this constitutes contraction of the muscular fibre. The stream of nervous influence being arrested, the magnetic state of the neuro-magnetic discs of the muscular fibres is for the time suspended, and so relaxation of the muscles takes place by the discs being allowed to separate from each other as far as their intervening substance will permit. According to the view now propounded of muscular contraction, the force with which it takes place must be greater towards the end than at the beginning of the action. This is quite contrary to the conclusion arrived at by Schwann from his carefully conducted experiments on muscular motion. But Schwann erred in applying to *muscular fibre* what he ascertained in regard to certain *entire muscles*, in which the component fibres are variously grouped and arranged in conformity with the duties the muscle has to perform. For the muscle having to overcome a greater resistance when it begins to act than afterwards, a greater number of fibres are so disposed as to come into play at the commencement—a smaller number at the end of its action. Vide *Lond. Med. Gazette*, Oct. 22nd, 1843. R. W.]

[834] Schwann made some accurate experiments upon frogs, in connection with this subject. Vide Muller's *Physiol.* vol. ii. p. 59, et. seq., and also Valentin and Henle (*Op. Cit.*), as well as the earlier and very valuable experiments of Prevost and Dumas, in Magendie's *Journal*, vol. iii.

direction and everything like marked wrinkling disappears, but they still preserve a slight degree of sinuosity, perchance in virtue of their inherent elasticity or tonicity.

§ 378. As already observed, the muscular motions fall naturally into two great physiological, and in part also, anatomical groups, viz., VOLUNTARY and INVOLUNTARY. 1*st*, Voluntary muscular motions are, for the major part, effected in vertebrate animals by means of cross-streaked muscular fibres. Muscles of this class may be regarded as the most perfect, and have this peculiarity, that by exercise they increase both in power and bulk; they are, therefore, susceptible of education. . From this it also becomes possible to isolate particular muscles, and groups of muscles, antagonists to one another, or of which the actions proceed in a kind of preordered harmony dependent on the nervous system. And on the other hand, we succeed in compelling particular muscles, and groups of muscles, which anatomically are either entirely unconnected, or are very imperfectly connected to simultaneous combinations of their activity. Those muscles that are seldom or never exercised, obey the mandates of the will very slowly and imperfectly, and totally neglected, many lose the capacity of contracting entirely,—this happens, for example, very constantly with the muscles of the external ear. (§ 299)[835]. 2*d*, AUTOMATIC OR INVOLUNTARY MUSCULAR MOTIONS,

[835] Dexterity in the greater number of handicrafts, or mechanical trades, is entirely due to practice or exercise, under the influence of which, certain muscular actions come to be performed with unusual rapidity, accuracy, and harmony. The more compound the motions, the greater the degree of rapidity necessary to their execution, the earlier and the more incessant must the exercise have been where perfection is attained. Of course, the greatest diversities occur among individuals and kinds, in reference to muscular actions. The human infant has to learn by slow degrees every motion it performs, and walking with uncertain steps is hardly acquired within a year or eighteen months from birth, whilst the chick and many mammals—the pig, the calf, the lamb, stand, walk, or run, almost from the moment they see the light. How slowly and imperfectly do the motions of the fingers go on in beginners on the piano and violin, of the feet in young dancers, &c. At first, too, the attention is too exclusively fixed upon the several acts of the necessary motions. By and by, the will and the motion constitute but a single act. Muscles that are not exercised seem to require a much larger amount of volition to bring them into play, and their contractions follow very slowly; of this every one may satisfy himself, by trying to make the palmaris brevis contract. There are naturally certain limits to the influence of exercise upon the isolation and combination of certain mus-

save in the case of the heart, are almost always connected with muscles and muscular fibres that are not cross-streaked[836]. They are incapable of any improvement, and are all apparently the results of reflected actions. The motions of the heart, respiratory organs, intestinal canal, and the excretory ducts of glands, belong to this category. The will has no kind of influence upon some of these motions (those of the heart and intestines), although passions and emotions, and intellectual operations, influence them in a very marked manner. In breathing, again, and the various motions associated with the act, such as laughing, sneezing, yawning, etc., the will has an undoubted influence; by a strong act of the will, they can even in some measure be suspended or prevented from taking place. In connection with such acts we have cross-streaked muscular fibres coming into play. Certain instinctive motions seem to stand in the middle, between voluntary and involuntary motions[837].

CHAPTER II.

OF THE COMBINED VOLUNTARY MOTIONS.

Of Locomotion.

§ 379. The first requisite to the locomotion of man, is the power to maintain the body erect. Mammalia, in general, can neither

cular motions, the grounds of which lie in determinate mechanical or organic conditions, as, for example, among the muscles of the eye. (Vide § 327, and Annotation).

836 A long array of pathological influences may also arouse automatical movements in voluntary muscles, a familiar instance of which we have in cramps, spasms, &c. Here, the motions are reflected.

837 To this head belongs the sucking movements of the new-born mammiferous animal, movements which are performed in a very remarkable manner among certain mammals,—the marsupialia,—by the extremely minute and almost rudimentary embryo. Farther details bearing upon the subjects of this paragraph, belong by rights to the General Physiology. The prime cause of all

stand upright, nor walk upon the two hinder extremities. In the human subject, the head in the erect position is beautifully balanced, immediately under its centre of gravity, upon the atlas or first vertebra of the neck[838]. The foramen magnum consequently lies much farther forwards in the base of the skull, than in any other creature. Even in the highest members of the monkey tribe, as in all other animals, the foramen magnum is placed so far back, that it presents backwards in front of the horizontally disposed vertebral column, so that it is only the powerful ligamentum nuchæ, and posterior muscles of the neck, that prevent the head from falling forwards and downwards, which its natural gravity constantly inclines it to do. In man, on the contrary, the natural tonicity of the muscles which connect the head with the spine, suffices to balance the head upon the top of the vertebral column, and the slightest excess of action in one or the other set of these muscles, inclines it to this side or to that; for in consequence of the elevated position of the centre of gravity, the head has always a disposition to fall over to one or the other side, or to drop forwards or backwards. The head and neck together can be bent forwards or backwards, about 75°, and to either side from 45° to 50° from the perpendicular line; the head consequently can be rotated through about the fifth part of a circle[839]. With the neck the head forms a two armed lever, the posterior and shorter arm being represented by the occiput, the anterior and longer arm by the sinciput and face.

In standing erect, the weight of the body is transmitted perpendicularly to the feet, which rest on the ground by the point of the heel-bone, and the fore ends of the metatarsal bones, particularly those of the great and little toes, as also by the points of the toes

the circumstances alluded to, inheres on the nervous system. Vide the Third Section of this Book.

[838] By far the most important work we possess upon locomotion, is that by the Brothers W. and E. Weber—*The Physiology of Locomotion—Mechanik der Menschlichen Gehwerkzeuge*, 8vo, Gotting, 1836, from which I have drawn freely in this and the next succeeding paragraphs.

[839] Vide Krause's *Manual of Anatomy*, 2nd ed., p. 461, to which admirable work I beg particularly to refer in connexion with the actions of the muscles, both severally and conjointly.

in general. The lower extremities are the props upon which the body rests. The place of the centre of gravity of the whole body appears to lie a few lines above the pubic arch, therefore somewhat above the transverse axis of the heads of the thigh bones, which are the points of support of the trunk. The pelvis itself, with the thighs fixed, represents a double armed lever, whose fulcra are in the heads of the thigh bones inclosed by the acetabula.

The vertebral column, when the body is erect, and at rest, is naturally sinuous, making without the slightest action of the muscles two curves forwards, and two backwards. But as the vertebral column from the weight of the masses attached to it anteriorly, particularly the viscera of the thorax and abdomen, is inclined to yield, or bend forwards; the great mass of the posterior spinal muscles is in a permanent state of contraction. The muscles around the acetabula would require nothing beyond the ordinary tonicity to maintain the trunk upright; but the mere rhythmical contractions of the heart, and especially the motions of respiration, alter the centre of gravity every instant, so that even in the attitude of the most perfect repose, the muscles have to be kept in a certain state of action—the muscles which keep the spine erect, act rhythmically and alternately with the muscles of respiration. The rotators of the thigh outwards, and several other muscles, counteract the trunk in its disposition to fall forwards[840]. The flexors of the thigh, and some of the extensors of the leg, again, oppose the trunk when it tends to fall backwards[841]. The muscles of the inferior extremity at large, indeed, of the leg and foot, as well as of the thigh, come into play in preserving the centre of gravity. In this way we account for the fatigue that is experienced from long continued standing, and the necessity of infants learning to stand, as they learn to speak. The centre of gravity may be thrown notably backwards, or forwards, as it is in balancing the body in different positions on one foot, or on both of the feet. The perpendicular, however, must never fall beyond the bounding line of the foot that is planted on the ground. The same law, in fact, obtains here, as

[840] To this number belong the glutæus maximus, pyriformis, obturator internus, gemelli, quadratus femoris, and adductor magnus.

[841] To this list belong the psoas magnus, iliacus internus, adductor longus and brevis, pectinæus, rectus femoris, sartorius, and gracilis.

in reference to the leaning towers which are met with in some parts of Europe, the centres of gravity of which, of course, always fall within the bases upon which they stand.

§ 380. The faculty of walking is connected immediately with the property which the two lower limbs have of swinging backwards and forwards from the trunk like a couple of pendulums. The construction of the hip-joint is of course a matter of the highest moment in this act; the pendulous limb must move in its socket with the least amount of friction possible. Experiments have shown that the pressure of the atmosphere suffices to keep the head of the thigh bone in the air-tight acetabulum; in other words, the weight of the atmosphere pressing upon the lower limb upwards and inwards, æquiponderates the weight of the limb. The lower extremities are consequently, and in fact, kept in their places by the same force which supports the mercury in the tube of the barometer[842]. The extremities upon which the trunk is balanced, are articular props, which by means of the hip, knee, and ankle, and other inferior articulations, can be bent into a zig-zag, and thereby lengthened and shortened. The trunk in the act of progression may be compared to a rod balanced upon an axis that passes through the two hip-joints. The body in this act must therefore be in every way analogous to the rod slightly inclined forwards, with which, balanced upon the point of one of the fingers, we advance. The tendency forward is to overcome the resistance of the air; it is therefore great in proportion to the resistance, that is, in proportion to the rapidity of the pace, and the force of the wind; it becomes as nothing when a current of air from behind æquiponde-

[842] It is easy to obtain satisfaction on this point, upon the dead body; let the whole of the muscles and parts that connect the thigh-bone with the pelvis, be cut away; let the capsular ligament even be cleared off up to the edge of the acetabulum, the head of the bone will not quit its socket. But let a small hole be now pierced with a fine awl from the internal pelvic aspect into the acetabulum, the moment the air finds an entrance, out drops the head of the bone, and remains suspended by its round ligament only; let the head of the bone be replaced, and the small hole that has been made be covered with the point of a finger, the limb will again be secured, and may be swung from side to side without fear of falling away, so long as the hole is kept covered; of course the finger being removed it drops away again immediately. See an account of this and many other experiments, in the work of the Webers already referred to.

rates the resistance of that which is encountered before; and, indeed, when we walk with a strong wind behind us, instead of bending the body forwards as usual, we bend it in different degrees back. The motions of the extremities are meantime so calculated, that they still oppose themselves to the tendency of the centre of gravity in the body, to sink vertically downwards. Either extremity in turn forms a prop, and with each step in forward motion an incessantly advancing buttress, so that the body, in fact, rests alternately upon, and is pushed onwards by, first one limb, and then the other. This is very obvious when we walk slowly. In each step it is easy to distinguish two periods: first, the body is poised upon one extremity, and then it rests for an instant upon both extremities. The advancing, say, the right limb, swings forwards, like a pendulum, having undergone a shortening by about the $\frac{1}{9}$th part of its length from the flexion of the knee-joint, with little or no muscular effort, inasmuch as we have seen that it is kept in its place by the pressure of the atmosphere. At the same moment the left extremity, by the straightening of the knee and hip-joint, pushes the pelvis and superimposed trunk so much forward, that the whole burthen is immediately transferred to the right extremity, now advanced and planted ready to receive it. It is only in very slow walking that the advancing limb completes the whole of the arc through which it is capable of swinging, for the duration of one of its vibrations extends through $\frac{2}{3}$rds of a second. In quick walking and running, each extremity performs no more than half a vibration, which occupies about half a second of time, during which, the other extremity has quitted the ground. The time during which each extremity is in contact with the ground in slow walking, is about $\frac{1}{3}$rd of a second. The longest ordinary step may equal about one-half of the entire span of the two extremities. In slow and measured walking, the trunk is carried erect, and the body has its greatest height; in running, the extremities are more bent, and the trunk inclined forwards in a greater degree, so that the height is considerably lessened;—the whole body is approximated to the ground[843]. In walking, the upper keep exact time with the lower limbs, being

[843] From Krause's admeasurements it would seem that the thigh may be bent forwards about 130°, backwards and straightened from 40° to 60°, about 90° outwards, and somewhat less inwards.

swung backwards and forwards, but always inversely, or in opposition as regards the two members of either side of the body,—with the right leg the left arm is advanced, the right is thrown back; with the left leg advanced the right arm swings forward, the left falls back; in this way is the equilibrium of the trunk maintained, and that alternate swaying motion from side to side is escaped, which we observe when walking is performed with the arms held close to the sides.

§ 381. All the other motions in space take place in accordance with the same fundamental principles as those of walking. In running the body is balanced essentially in the same way as in walking, but with modifications to suit the particular circumstances. In walking, for instance, there is a distinct limit set to the speed, length of step, etc.,—the space we measure at each step must be spanned by one limb, whilst the other is fixed perpendicularly upon the ground; and then these steps cannot be repeated with an accelerating velocity, inasmuch as the number of steps in a given time cannot exceed the double of the vibrations which the limb as a pendulum would perform in that time. In running, however, we make at once more numerous and longer steps than we do in walking, and are not fettered by the circumstances that restrict us there, although we can also run slowly; if we choose, indeed, we can, whilst we perform the motions of running, make less speed than we can by quick walking. The grand difference betwixt walking and running lies in this, that in running the feet are planted in strict succession, one after the other, on the ground, and there is a particular moment in every step when both feet are raised from the ground at once, whilst in walking there is a particular moment in each step when both feet are upon the ground together,—one is not raised until the other is planted. The greater rapidity of motion in running is attained: 1*st*, By the longer steps that are taken, the body being literally projected into the air, and the space measured being thus greater than the simple span of the legs could accomplish. 2*d*, By the greater number of steps that are taken in a given time, both legs swinging here at the same moment, whilst in walking they can only swing alternately. [In running, too, the legs are shortened by being much bent at the knees, whereby the length of

the pendulum which they represent is lessened, and its vibrations are rendered in the same proportion quicker][844].

§ 382. In leaping, the lower extremities act in the manner of articulated levers which tend to push the body upwards. The body is momentarily projected from the ground by a force superior to that which retains it there. The upper extremities are at the same time thrown upwards by their own muscles, and so make the body lighter by the whole amount of their weight. In leaping, the lower extremities are bent at the knees and ankles, by which the point of gravity of the body is brought nearer to the ground. The sudden contraction of the extensors then develops the force which, hindered by the firm ground from acting downwards, acts upwards, and raises the body. The power is greatly augmented by the rapidity of the muscular contraction, and is principally acquired by the action of the gastrocnemii and solei muscles.

Motions in Mastication and Deglutition.

§ 383. The articulation between the lower jaw and the skull is one of the freest in the body; the jaw does not only move like a hinge, but can be carried for some way forwards, and to either side; it can also be moved, although in a less degree, backwards. By this means are those rotatory or grinding motions possible, in which the essence of chewing consists[845]. The lower-jaw is a bent lever, which has its fulcrum in the articular surface of the temporal bone. In repose, the articular head of the jaw sits fast in its socket; but with the slightest biting motion, such as is made when food is seized and held fast with the incisors, the lower-jaw is first

[844] The brothers Weber have found by measurements, that in running the steps are on an average twice as long as they are in walking, and that the number of steps in a given time in each kind of progression stand to each other in the proportion of 3 to 2.

[845] The comparison of this joint in the series of mammalia is interesting; it offers numerous varieties, each of course in admirable harmony with the wants and mode of life peculiar to each animal—in the carnivora, in the ruminants, in the gnawers, everywhere it is modified. Vide my observations in the New Edition of Söemmerring. The structure of the human lower-jaw gives us an assurance, that man by his organization is fitted to live alike on animal and vegetable substances, or on a mixture of the two.

depressed lever-wise, whereby the articular head slips forwards; but with the act of seizure, the reverse movement takes place, and the articular head, besides tumbling upon itself, slips back into the depth of the socket, by which the scissor-like motion of the incisors is effected. In chewing with the grinding teeth, again, a slight lateral and rotatory movement takes place, in which the articular head of the lower jaw describes little circles upon the opposed articular surface of the temporal bone. The act of mastication is a very complicated one, a great many muscles contributing to it, as well in reference to the motions of the jaw, as to turning the morsel, and keeping it continually between the teeth[846].

§ 384. In the process of deglutition, several steps or acts are readily distinguished, in which the muscles of the lips, the tongue, the soft palate, and the pharynx, are successively and simultaneously active. In the first act the morsel collected into a ball by the tongue, is pushed by this organ backwards and upwards, against the palate, and behind the anterior palatine arch. In the second act the tongue is drawn backwards, and the glossopalatinus, or constrictor isthmi faucium muscle, contracts like a sphincter behind the morsel. The larynx meantime is raised, and the epiglottis by this act, and the bending of the root of the tongue backwards and downwards, is applied over the entrance into the wind-pipe, so that the morsel is safely conducted over it. The posterior arch of the palate (including the pharyngo-palatine muscles within its folds) now contracts until its opposite sides almost touch,—a mere narrow slit alone remaining between them; the whole upper part of the fauces is narrowed, and the mouthful is pressed continually onwards. The superior muscles of the soft palate—tensores veli palatini, and levatores palati mollis, have, farther, raised the velum palati somewhat upwards, and fixed it. The constrictors of the upper part of the pharynx now push the morsel into the œsophagus. At this point voluntary is replaced by involuntary motion, and the third act in the process is accomplished by the contraction of the suc-

846 The lower jaw is opened or separated by the digastrics, mylohyoidei, and geniohyoidei, and shut by the masseters, temporals, and internal pterygoids; it is moved laterally by the external pterygoids. These four muscles are the proper muscles of mastication. The tongue, the lips, and the cheeks, by means of their several muscles, push the morsel between the teeth.

cessive fibres of the œsophagus, which follows irresistibly as a reflex action in consequence of the stimulus of the morsel in the canal which it is traversing. The will is not altogether without influence upon the muscles of the upper part of the œsophagus, as any one may satisfy himself by experiments in his own person. When swallowing motions have been made a few times in succession without food in the mouth, however, the power to continue them becomes exhausted, and we must rest for a while before we can renew them. The action of the œsophagus is totally abstracted from the influence of the will. The contraction of its successive circles of fibres generally takes place with great rapidity, and insensibly; when the mouthful that is swallowed is very large, however, the contraction is more tardy, and is painful; a good half-minute may elapse betwixt the time that the morsel is received into the pharynx, and that at which it reaches the stomach[847].

Respiratory Motions.

§ 385. The morphology or doctrine of the forms exhibited by the respiratory apparatus, and the chemistry of respiration, have

[847] Dzondi has treated the subject of deglutition with great perspicuity. See his work, entitled, *The Functions of the Soft Palate—Die Functionen des weichen Gaumens*, Halle, 1831. [The most complete observations which we possess on the muscular sheath of the œsophagus, are those of Mr. Gulliver, (vide *Proceedings of the Zoological Society* for September, 1839, and June 14th, 1842). In man, the quadrumana, some of the felidæ and viverridæ, the seal, the horse, and the porpoise, the last portion or stomachic end of the gullet is not covered with the muscular fibre of animal life; but this fibre invests the whole length of the gullet, and sometimes extends a short way on the cardiac end of the stomach in the insectivorous feræ, the ursidæ, ruminantia, rodentia, and in certain fishes; in several birds and reptiles, the muscular fibre of animal life forms no part of the œsophageal sheath. In the streaked muscular fibres of the gullet, Mr. Gulliver found all the anatomical characters of the muscular fibre of animal life, which no completely involuntary muscle, not even the red flesh of the heart, has yet been found to possess. If, therefore, we may judge of the motory power of the œsophagus from the structure of its sheath, we must conclude, that in many vertebrate animals the whole length of the tube is capable of voluntary motion, or something very like it; in several cases, as in that of man, the lower or posterior part of the gullet is not under the influence of the will, while in others, the motion of the entire tube must be quite involuntary. R. W.]

already been fully considered (§ 165—183). All that remains for us in this place, is to take a particular view of the mechanical conditions needful to respiration; for we see that the apparatus from the beginning to the end of life is in state of incessant rhythmical motion, in the course of which a certain measure of atmospheric air is taken into the lungs, and a certain measure of air contaminated with carbonic acid especially, and loaded with moisture, is returned. The first division of the act constitutes inspiration, the second, expiration. The rhythm of the breathing varies greatly at different times, and in different circumstances; it is influenced by age, sex, watching and sleeping, health and disease, rest and exertion, etc. On an average, an adult makes about twenty respirations in a minute[848]. Each inspiration is followed immediately by an expiration; there is then a brief pause, after which follows the next inspiration, and so on. The quantity of air taken in at a breath varies much in different individuals; it is in the ratio of the capacity and healthy structure of the lungs, and therefore in proportion to the stature, the general power, habits of exertion, etc., of the individual. Speaking very generally, it may be said that from 15 to 20 cubic inches of air are taken in and rejected from the lungs at every breath, and that in the course of twenty-four hours, from four to five hundred thousand cubic inches of air are consumed[849].

§ 386. The lungs of man and animals lying closely applied to the walls of the thorax,—no vacant space being interposed between

848 The consideration of individual varieties, according to age, sex, state of health, &c., is within the province of the general and applied physiology. In the new-born infant the number of inspirations is nearly double that of the adult, consequently, about 40 in the minute. Large mammiferous animals, also, make fewer respirations than small; whilst the whale, according to Scoresby, takes from 4 to 5 breaths in a minute, the dog, cat, and rabbit take from 20 to 30. The number, however, is greatly varied by external states and circumstances.—During sleep the breathing is not so quick by a third, and even by one half, as it is when we are awake. Burdach, in his Physiology, has given a summary of the statements of different observers, vol. vi. p. 429.

849 The numbers here are very differently stated by different observers. Whilst Abilgaard estimates the quantity at from 3 to 5 cubic inches; Davy states it at from 10 to 13, Allen and Pepys at 16, Herbst at from 16 to 25, and Menzies and Bostock at 42. Herbst in a paper *On the Capacity of the Lungs in Healthy and Diseased States*, published in Meckel's *Archiv*, for 1828, has given a summary of the estimates of different writers.

them—the capacity of the chest must necessarily enlarge during inspiration, and diminish during expiration. The lungs themselves, from the trachea to the last vesicular terminations of the bronchi, are more or less distended with air; they are never completely emptied, even in the most prolonged or forced expirations; and after death they still contain a quantity, which has been estimated variously at from 90 to 120 cubic inches. From experiments on the dead body, it has been found that the lungs distended to their utmost capacity, will contain about 150 cubic inches of air; in ordinary breathing, therefore, we see that no more than about a sixth part of their contents can be renewed each time. The fresh air inspired, must of course mingle with the air which is already contained in the lungs, and doubtless, a portion of that which has just been assumed is again rejected with portions of that which had already been some time in the lungs. From this we perceive that the influence of the air upon the blood is of a continuous or incessant nature; it is not a process that goes on only at the times of inspiration[850].

§ 387. In man and the mammalia, the chest is expanded during inspiration by the elevation of the ribs, and, at the same time, deepened by the descent of the diaphragm. The ribs, which have a double point-d'appui on the bodies and transverse processes of the vertebræ, are drawn upwards and outwards, by which their inferior margins are partially turned upwards. In tranquil breathing, the diaphragm appears to be the active instrument in inspiration; by the contraction of its muscular fibres it is drawn downwards towards the abdominal cavity; in expiration it relaxes, and is pushed up again into the cavity of the chest, by the resilience of the thoracic

[850] Herbst assumes with Davy, that after the greatest expiration, about 41 cubic inches of air still remain in the lungs, and that the capacity of these organs in the adult male is between 220 and 260, or even 280 cubic inches. He could not, however, force more than about 186 cubic inches of air into the lungs taken from the body of an adult, without risk of tearing them. In the lungs of four persons who had died a natural death, Goodwin found 109 cubic inches of air in each. All these statements must be taken as mere approximations; the process of respiration proceeds with very different rates of rapidity in different circumstances—the act, always necessary, is much more so at one time than another.

grating and the action of the abdominal muscles. In somewhat more vigorous breathing, the intercostal muscles come into distinct action[851], raising each successively lower rib towards the superior fixed one; in expiration, these muscles relax of course. The first pair of ribs, which anteriorly have the least mobility of all the pairs, but posteriorly enjoy some greater extent of motion, require more powerful muscles both to raise, and to fix them; the scaleni muscles in especial, act powerfully upon them, and tend to raise and approximate them to the neck. In very deep and laborious inspirations, in which the body must be fixed by being supported on the hands in a sitting posture, many other muscles come into play—the serrati antici majores, pectorales minores, sternomastoidei, and subclavii, and, farther, the whole of the muscles that raise the shoulder-blade and clavicle. In all respiratory motions the sternum is moved alternately out and in, or forwards and backwards. Active muscular efforts occur in expiration only when it is impeded by any cause—when there is some obstacle to the escape of the air from the chest. The elasticity of the thorax in general suffices to empty the lungs to the extent that is necessary, and this elasticity comes into play the moment the respiratory muscles have ceased to act. In more active expiration, the abdominal muscles are called into requisition, and they act powerfully, as well by dragging the edges of the ribs downwards, as by pushing the diaphragm supported upon the convexity of the liver upwards into the thorax[852].

§ 388. In ordinary breathing, the air finds access to the lungs entirely through the nostrils; so does it also when the breathing is more vigorous than usual; in which case the alæ nasi are observed to be in constant action, being powerfully dilated at each inspiration,

[851] Besides the diaphragm and the intercostals, the levators of the ribs and posterior serrated muscles also come into action here; the antagonists of these being the triangularis sterni, and the quadratus lumborum.

[852] Theile has proposed it as possible, that the two layers of intercostal muscles may act as antagonists to each other, that the external may be muscles of inspiration, the internal muscles of expiration. See his article—*Athmung*, *Respiration*, in Schmidt's *Encyclopædie*. [The effect of either layer of these muscles must depend entirely upon that which is the fixed point in the thorax at the moment of their action. In a general way the first rib is the fixed point, and the internal layer then tends to raise the ribs, and expand the chest as effectually as the outer layer. R. W.]

and contracted again at each expiration. With each inspiration the trachea is depressed by its extrinsic muscles, and the rima glottidis and larynx generally are widened by the intrinsic muscles. The trachea and rima glottidis, again, contract upon each expiration. The contractile and partly true muscular fibres of the trachea, unquestionably assist in this latter action; these fibres, indeed, accompany the ramifications of the bronchi to their extremities, and as it seems even surround the several air-cells of the lungs, (Figs. CLXXV and CLXXXII,) so that they must be the active agents in emptying these of the air they contain, whilst they dispose the lungs at large to contract[853].

§ 389. To the number of respiratory movements must be reckoned various modified motions, which, like the breathing itself, are partly dependent on the will, partly abstracted from its influence. All these motions are referable to inspirations and expirations, but with alterations in the rhythm. In what is called hawking, the mucus that has accumulated in the trachea, or about the fauces, is forced up by means of powerful expirations, aided by the special action of the velum palati, the air passing through the mouth; in blowing the nose the air is forced by a strong expiratory effort through the nostrils, the mouth being closed. In sighing, which happens involuntarily or unconsciously, a prolonged inspiration is followed by a hasty expiration; snoring is occasioned by the flapping of the velum palati, and occurs during deep sleep when the mouth is partially open, and particularly when the person is lying on his back. In efforts of various kinds, in straining at stool, etc., the chest after a somewhat full inspiration, is fixed, and the breath held for a moment, suddenly the laryngeal muscles relax, and the expiration follows short and generally with an audible noise.

[853] Of the elasticity of the terminal vesicles of the lungs, conviction may be obtained by examining thin slices of the organs under compression with thin plates of glass. The degree in which the lungs themselves are active in respiration has afforded matter for controversy from of old. Haller denied them any contractile power; Rudolphi, on the contrary allowed, and Jo. Müller refuses them contractility. Krimer and Valentin have observed actual contractions in the trachea at least. Vide Theile, in Söemmerring's *Anatomy*. [In many animals, as in the horse, the elastic tissue investing the entire surface of the lung, as with a capsule, is no doubt one of the agents in expiration. Vide Annot. 331. p. 360. R. W.]

§ 390. The involuntary respiratory motions are of the reflex order, and take place either under the influence of local peripheral stimulation, or of impressions made upon the sensorium. Sobbing is nearly of the same nature as sighing, the act, however, being frequently repeated, and taking place by starts; in this act the diaphragm appears to be particularly active. Sneezing is a spasmodic expiration following a more gradual inspiration, at least in the beginning of the bout. In yawning, a long-drawn inspiration is followed by a like, or even longer expiration, at the same time that various muscles of the face come into action, particularly the digastrics of the lower jaw, which are in some sort spasmodically affected, and open the mouth widely. Coughing is a reflected spasmodic motion in consequence of an irritation—such, for example, as an accumulation of mucus in some part of the air passages, or from consent or sympathy with other parts, which receive branches from the pneumogastric nerve—the stomach, etc. In this act, upon an inspiration of variable extent, a succession of syncopated expirations follow each other with rapidity, the barking sound being due to the action of the muscles of the larynx, which from a state of powerful tonicity, suddenly relax at intervals, and suffer the air to escape in jets. Crying consists in alternate deep inspirations and expirations, the former being often impeded by a semi-spasmodic state of the muscles about the rima glottidis, whereby the inspiration becomes crowing, and syncopated, or divided into several stages. In laughing, the expirations take place by fits, the muscles which regulate the laryngeal orifice relaxing and contracting alternately. Both in weeping and laughing, as all the world knows, the muscles of the face are powerfully affected, though the expression is very different in each; tears belong to grief especially, but hearty laughter sheds tears also. All these motions are greatly modified according to the degree of violence, or energy with which they take place; they are also frequently associated—sobbing and weeping, for example; and they are also influenced by the sensorium, which, as in the case of the respiration, if it does not control them entirely, can still increase or moderate them to a certain extent.

Of the Voice and Speech.

§ 391. A competent knowledge of the anatomy of the larynx, and of the physical conditions needful to the production of sounds, is implied in entering on the consideration of the physiology of the vocal organs. The production of sounds by a particular organ is connected in all the higher animals with a respiratory system consuming air. It is only in comparatively low grades, that we note the production of sounds associated with the intestinal canal, and the external horny skeleton[854]. We observe a true voice, more or less perfect, only in amphibia, birds, and mammals[855]. Here the larynx is the instrument in which, by the agency of the air, pulses are produced that reach the ear as sounds. The human larynx is, indeed, a musical instrument of great perfection; by certain muscular motions it is brought into the state of tension necessary to the production of tones, and by the combination of different muscles, all the sounds from high to low, which we distinguish in speaking and singing, are engendered. The doctrine of sounds, and their formation, like that of vision and hearing, has an extensive physical substratum, to illustrate which, is among the objects of elementary works on physics[856].

[854] The cooing or croaking noise of the loach—Cobitis fossilis, for example, and the chirruping of the cricket and grass-hopper. On the means by which these sounds are produced, see my *Elements of Comp. Anatomy*, p. 237.

[855] I have not thought it necessary to include the voice of the lower animals in my summary in this place. I refer to my *Comparative Anatomy*, and *Icones Zootomicæ;* to Henle's monograph *On the Comparative Anatomy of the Larynx*, 1839, and to Müller, *On the Compensation of Physical Forces in the Human Organ of Voice, &c.*, 1839.

[856] Müller has entered at great length into the physical conditions needful to the production of sound in his *Physiology*, and has carried out the principle consigned in the important work of W. Weber, *On the Theory of Reed-pipes*, in its particular bearing upon the formation of the human voice. Müller's *Treatise on the Physiology of the Voice* is by far the best we have, and I have taken him for my guide in these paragraphs. Among those who have occupied themselves with the physics of the voice, Savart and Cagniard Latour deserve particular mention. See also Lescovius, *On the Theory of the Human Voice*, Lips., 1814; Bennati, *Recherches sur le Mechanisme de la Voix Humaine*, Paris, 1832; and Haeser, *On the Human Voice*, Berlin, 1839. Among the Physiological Elemen-

§ 392. General observation satisfies us that the voice is formed in the rima glottidis—neither above nor below it. 1*st*, When an opening is made below the larynx into the trachea of an animal, the voice is extinguished; but it is recovered if the orifice be closed[857]. Cases have occurred in the human subject, in which a fistulous opening has existed under the thyroid cartilage into the wind-pipe, and where the facts just mentioned have been noted on the alternate opening and closing of the hole with the point of a finger[858]. On the contrary, a wound made fairly into the gullet above the chink of the glottis, or even implicating the superior bands of this part, and cutting away a portion of the arytenoid cartilages, is not followed by extinction of the voice. 2*d*, The larynx removed from the body of a man or animal, if blown through from the inferior extremity, can be made with a little management to produce tones that bear a certain resemblance to those of the living being. This happens when the whole of the trachea is retrenched, when the epiglottis, and even the superior cordæ vocales, the ventricle betwixt the inferior and superior cordæ vocales, and the large superior portions of the arytenoid cartilages, are taken away[859].

§ 393. Everything satisfies us of the correctness of that view, according to which, the trachea is regarded as analogous to the conduit from the wind-chest of a musical instrument that speaks by wind—such as an organ-pipe. All the parts above the rima glottidis,—the fauces, mouth, and nostrils, are as the part of the organ-pipe which stands above its mouth, and which have nothing to do in engendering the tone, but which modify it powerfully. The parts that are of the highest consequence are the ligamenta thyreo-arytenoidea inferiora, seu chordæ vocales, which are pre-

tary works, those of Mayo and Magendie may be consulted, in connection with the important appendices to the German translations, by Heusinger. Bindseil has also treated the physiology of the voice and articulate speech with great ability in his work *On Language — Allgemeine vergleichende Sprachlehre*, Hamb., 1839.

857 Magendie instituted many experiments of this kind—*Physiology*.

858 Magendie had an opportunity of observing a man who had a fistulous opening into his wind-pipe, and who could not speak unless he wore a pretty tight cravat about his neck. Cases of the same kind have been seen by many others—Dupuytren, Bell, &c.

859 This, from Müller's experiments.

cisely the parts between which lies the elongated slit called rima glottidis. These chords are the parts which are thrown into vibration by the column of air that passes rapidly betwixt them, so that the human larynx bears the most perfect analogy to a reed-stop with a double membranous tongue. The lungs and bronchi represent the wind chest, from which the air is expelled through the narrow rima glottidis, the ligaments or chords of which, like the reed in an organ-pipe, or clarionet, are immediately thrown into vibrations, which being communicated to the issuing column of air, the sound with its peculiar quality is produced[860].

§ 394. The vibrations of the chordæ vocales depend on their elasticity; their tension is regulated by the action of the thyreo-arytenoidei muscles especially. The elasticity of the chordæ vocales is owing to the elastic tissue of which they consist[861], and it is in virtue of their structure that they are enabled to vibrate like a couple of extended membranes. The stretching or tension is effected by the motions of the thyroid upon the cricoid cartilage through the contractions of the cryco-thyroidei, as also by the motions of the arytenoid cartilages from the actions of their proper muscles. The rima glottidis is made narrower by the approximation of the arytenoid cartilages by the action of the musculi arytenoidei proprii, and it is enlarged by the separation of the arytenoid cartilages

[860] This comparison of the vocal organ of man and mammalia to a wind instrument with a reed, is now generally supported. Dodart, Magendie, Cagniard Latour, and Jo. Mueller, have in particular shown its identity with reed-stops, having membranous tongues. The most important objections to this view have been made by Savart, who compares the human organ of voice to the little instrument called a bird-call, maintaining it to be in its essence a libial pipe with walls susceptible of divers degrees of tension. He, as well as all who espouse his, or an analogous theory, maintain that the air alone is the sonorous body. Another view, in which the chordæ vocales are regarded as the only sonorous parts, and that the larynx is therefore to be compared to a stringed instrument, (whence the name chordæ vocales), took its rise with Ferrein, and acquired a certain reputation, in consequence of Haller having lent it the weight of his authority. It has had no advocate in recent times. All our knowledge leads us to regard the voice as the product of the joint vibrations of the chordæ vocales and column of air in the trachea, larynx, and mouth,—the whole of the parts in short which bound the vibrating column.

[861] For an account of the structure and properties of the elastic tissue, vide Henle's, Bruns', Gerber's, and other elementary works on general anatomy, and § 403.

effected by the crico-arytenoidei postici. Opportunities have occasionally occurred of observing the alterations which take place in the state of the rima glottidis in the living subject[862]. In the state of repose, the breathing being slow and regular, it appears to be triangular, or lancet-shaped, the base being backwards, and the sides formed by the inner aspects and anterior processes of the lower portion of the arytenoid cartilages. (Vide Soemmerring's *Icones Organorum Gustus et Vocis*, Fig. XX.) Anteriorly the greater part of the rima glottidis is formed by the chordæ vocales themselves, which are attached to the anterior processes of the arytenoid cartilages. The only part of the rima glottidis susceptible of proper vibration, is this anterior portion bounded by the elastic chordæ vocales. When a sound is produced, the rima glottidis is so narrow that nothing more than a mere linear chink remains. When the nerves which supply the muscles which have been mentioned above are divided, the voice is destroyed.

§ 395. The latest experiments on the formation of the voice with natural and artificial larynxes, satisfy us that the inferior vocal chords give pure and full tones upon being blown through, when the rima glottidis is narrow enough. The tones bear a great resemblance to those of the human voice, and are also very like those that are elicited from an artificial larynx, having vibrating tongues made of portions of the moist coats of an artery. The ventricles of Morgagni, the superior vocal chords, and the epiglottis, as also the posterior wall of the larynx, vibrate powerfully at the same time, and, doubtless, strengthen the sound. By merely altering the tension of the chordæ vocales, tones to the extent of two octaves can be produced; when the tension is great the tones are high, shrill, or screaming; when it is slight, on the contrary, the tones are deep or grave; the lowest bass notes are consequently produced along with the greatest state of relaxation of the vocal chords induced by the retraction of the thyroid cartilage. The chordæ vocales which vibrate through their entire depth, are not only com-

[862] Rudolphi, Mende, Mayo, and Bell, in particular, have communicated observations on such cases. Kempelen, *Mechanism of the Human Voice*, Vienna, 1791, maintained that the rima glottidis cannot be more than $\frac{1}{12}$th or $\frac{1}{10}$th of a line open when sounds are to be formed; observation in the living subject has confirmed this view.

pletely relaxed in their states of greatest relaxation, but in the state of repose are wrinkled or folded. By the mere force of the air urged over them, however, they are stretched, and by this acquire the degree of tension necessary to enter into vibration. In the ordinary state of repose of the larynx, when the chordæ vocales are neither in a state of tension, nor of such relaxation as to fall into folds, the parts are in the condition most favourable to the production of the usual medium or speaking voice, which is generally pitched midway between the deepest and the highest pectoral tones. In the falsetto, or head voice, the upper marginal parts of the chordæ vocales alone appear to vibrate. The height or acuteness of these tones depends on the high state of tension of the chordæ vocales. The sounds elicited from the female larynx are in general higher than those that proceed from that of the male. The length of the chordæ vocales in the two sexes differs; whether in the state of action or repose, they are to each other in the ratio of about 3 to 2. We have as yet no comparative measurements of these parts in the larynxes of distinguished male and female vocalists. The ventricles of Morgagni appear to have no other object than to leave the chordæ vocales free externally, to the end that their vibrations may be unimpeded. The strength and quality of the voice depend greatly upon the state and condition of the passages above and below the reeds or parts that immediately give it to existence—the chordæ vocales[863].

[863] In the above paragraph I have given the briefest possible summary of the results of Müller's researches. In the work of this distinguished physiologist, *On the Compensation of Forces, &c*, may be found figures of the apparatus necessary to experiments,—artificial larynxes, &c. Cagniard Latour some time back laid an account of his experiments illustrative of mechanism of the human voice, before the Royal Academy of Sciences of Paris, and has given an abstract of his conclusions, in No. 376 of *l'Institut.* This philosopher lays great stress on the sinuses of Morgagni, which he thinks do not exist for the sole purpose of permitting the chordæ vocales to vibrate freely, but which, he says, perform an acoustic office in virtue of the mass of air they include; he concludes, in fact, from his experiments, that these sinuses are the seat of very energetic vibrations, that they contribute mainly to bring the whole of the parts composing the larynx into a state of vibration, and also impress particular qualities upon the sounds emitted. These views he illustrates by means of a wind instrument of his invention, which he calls the sirene. He thinks that the vibrations which are productive of the voice, are in part molecular vibrations—vibrations of sur-

§ 396. Besides the sounds that are produced in the larynx, there are others of a much more limited and less significant nature, that have their origin in the mouth—there are oral as well as laryngeal sounds due to the vibrations of soft membranes. To the class of oral sounds belong those that are heard in snoring and hawking (§ 389). The two folds of the palatine arch are here thrown into vibration by the stream of air that is passing over them, and literally become for the time double membranous tongues or reeds. The lips may also be made to comport themselves like vibrating membranes or reeds, and so to serve for the production of sounds; the lips are the reeds made use of by players upon all the varieties of horn and trumpet we possess, from the ophicleide and trombone upwards. In whistling, the lips do not vibrate—the column of air is thrown into vibration by rubbing over the surface of the lips; whistling sounds of the ordinary character are produced with a small perforated disc of wood, or cork, betwixt the lips. It is to be understood that in all the tones and sounds produced by the proper vocal apparatus and the adventitious tube with which it is connected, such as speech, etc., vibrations of the columns of air and surrounding parts take place together; it is, however, extremely difficult to determine the relative share which each has in the production of the determinate tone or tones.

§ 397. All the articulated tones or sounds which form the basis of speech, are produced under the conjoint influence of the larynx, fauces, and mouth. The sounds are very far from being all exactly alike in every language that is spoken by man; the great diversities of tone and character, indeed, in different languages, satisfy us of the infinite variety that is possible. The usual division by grammarians of articulate sounds into guttural, lingual, and labial, is not altogether correct. In the majority of instances, the whole or the greater number of the organs included in the mouth, cooperate in producing each articulate sound. The vowels alone are primarily formed between the vocal chords; here, the mouth is indiffer-

rounding solid parts, before they are äerial vibrations. In all that has reference to experiment, I imagine that there is little room for addition to what has been done by Müller. Perhaps the only point that has not been taken into sufficient account of late, is the vibration of the column of air in the conduits above and below the vibrating tongues.

ent, or nearly so, whether the sounds be uttered loudly or softly. The vowels are articulated with the slightest effort and least practice, and on this account are always first learned by children. The consonants, which serve for the connection of the vowels, are more difficult of articulation, extensive muscular combinations being indispensable in the act; children therefore only acquire them slowly, and often with the aid of tuition; some consonants, indeed, are never properly mastered by certain individuals in the course of their lives. The consonants of foreign languages, too, which we learn when we are no longer children, often puzzle us in spite of our best efforts to conquer them—we have not been accustomed to make use of the precise muscular combination that is required to elicit them[864]. For the same reason it is found more difficult to acquire a language in proportion to the number of its consonants. The Sclavonic tongues are extremely obdurate in the mouths of the Celtic and Gothic nations of Western Europe. SINGING is a modification of speech, consisting in a succession of acuter or graver tones, with a dwelling upon the vowel sounds, in the production of which, the muscular action is more complicated and perhaps energetic; whence the fatigue that is experienced in singing for a length of time.

Animals have a voice, and they sing, but they have no speech, they have no language. To the production of language, therefore, thought is indispensable, and that to an extent such as can coexist only with the very high organization of the human brain. Idiots from their birth, therefore, do not learn to speak, or they learn imperfectly, in a measure commensurate with the manifestation of psychological power. Language may be looked on as the highest kind of play or mimicry; it is a communication of our thoughts in articulate sounds produced by highly complicated muscular movements. The relations of the voice and speech to physical phenomena, belong to the General Physiology[865].

864 The *th* of the English, the *ch* of the Germans, the *ch* of the Swiss, the *g* of the Spaniards, are examples. *R* is one of the consonants that are learned with difficulty; children always substitute an *l* for it; certain persons slur it so long as they live, and in some languages, the Chinese, for instance, it does not exist.

865 The *Physiology* of Müller, and the work of Bindseil, already quoted, will

CHAPTER III.

OF THE INVOLUNTARY MOTIONS.

Of the Heart, and the Phenomena of Motion occurring in the Vascular System.

§ 398. In man, the mammalia, birds, and the crocodile among amphibia, the heart is formed on the same essential plan; it consists of two distinct auricles, and of two equally distinct ventricles [866]. When the thorax of a living animal is laid open [867], the two auricles and the two ventricles are observed contracting and dilating alternately, the two auricles acting synchronously, and then the two ventricles. These contractions depend on the abbreviation of the multitude of muscular fibres of which the heart is composed [868]. The first movement is that of the auricles, which contract rapidly and shortly, immediately upon which, without remarkable interval

be advantageously consulted for more extended information on the topics embraced in this important Chapter.

866 The beat of the heart, and therefore the mechanism of the heart's movements, are essentially the same in all the four classes of vertebrate animals, so that a frog may be selected with perfect propriety for the study of the phenomena; the auricles here are double, indeed, and the ventricle is single, as in the majority of the amphibia, and all fishes, but the acts are the same as in man. The active participation of the muscular fibres in the systole becomes evident in the excised heart of the frog: during the systole the heart is seen to rise from the surface upon which it is laid, and in the diastole to sink down again. Vide Oesterreicher *On the Circulation*, (in German,) Nürnb., 1826, p. 33, a work in which the literature of this Chapter will be found given with great completeness.

867 It is by no means necessary to lay open a warm blooded animal alive. The creature may be pithed, or poisoned with one of the narcotic poisons, and the circulation kept up for three-quarters of an hour and more, by means of artificial respiration.

868 The muscular substance of the lymphatic hearts of amphibia is transversely streaked. The one in the sciatic region of the frog affords a subject for examination accessible at all times.

follows the contraction of the ventricles, a slower process, and of about twice the duration of that of the auricles. After this there is a pause. The contraction of the auricles accomplished, they immediately fill with blood again, and increase in size, their muscular fibres having relaxed; this moment of repose constitutes the diastole of the auricles, as that of contraction constitutes their systole. Precisely the same phenomena take place in the ventricles, the systole of which occurs at the beginning of the diastole of the auricles. The pause in the action of the heart happens along with the conclusion of the diastole of the auricles, and continues through the whole of that of the ventricles. The stroke or impulse of the heart, which is due to the ventricular systole, therefore, falls between two pauses. In the interval betwixt two impulses the whole heart contracts once, and empties itself of the entire charge of blood which it contains. The systole of the auricles is accomplished very rapidly, and in silence; it forms a kind of preliminary to the second act in the beat of the heart, which lasts much longer. During the systole, the cavities of the heart diminish; during the diastole they enlarge. With the ventricular systole there is a distinct alteration of place: the apex of the heart rises, or is projected forwards and upwards, from the spine towards the anterior parietes of the thorax, against which it strikes, in the normal state, betwixt the fifth and sixth ribs of the left side. The impulse of the heart is therefore felt most forcibly in this intercostal space. In the course of the systolic lever-like motion of the heart now indicated, there is, farther, a slight turning of the organ upon its axis from left to right; with the diastole the motion is reversed, and the organ falls back, or sinks down upon the spine. This rotation upon its axis is the main cause of the alternate rise and fal of the apex of the heart, and consequently of the impulse, and depends itself on the [arrangement of the muscular fibres and] influx and efflux of the blood[869].

869 Vide the late memoir of Kürschner on the impulse of the heart, in Müller's *Archiv* f. 1841, as also his article Auscultation in Schmidt's *Encyklopædie*, B. i, in which the opinions of different writers, Hope, Skoda, &c., are passed in review. Vide also *Reports of the British Association* for various years, particularly 1835, 1836, 1838, 1839, and 1840, for much valuable information on the motions and sounds of the heart. [I believe the impulse of the heart to be mainly due to the alteration that takes place in the shape of the organ, when in

§ 399. When the ear is applied to the chest in the region of the heart, certain peculiar sounds are heard, one of them coincidently with the pulse in the arteries. For every beat of the pulse or stroke of the heart, however, two sounds are heard. The first is dull and extended. This is perceived at the same moment that the apex of the heart impinges against the ribs, and is therefore synchronous with the systole of the ventricles. It is difficult to render a precise and satisfactory reason for this sound; perhaps it does not depend on any single cause or circumstance; it is certainly connected in a very particular manner with the progressive contraction of the muscular compages of the ventricles, from the basis towards the apex of the heart, and it is probably strengthened by the contact of the apex with the thoracic parietes, [as well as by the closure of the auriculo-ventricular valves;] it cannot depend on either of these latter circumstances singly, inasmuch as it is still distinctly heard when the thoracic parietes are removed, [and also when the auriculo-ventricular valves are destroyed][870]. The second, weaker, and at the same time shorter, sound follows the first, after a brief interval, It coincides with the beginning of the diastole of the ventricles. It is audible when the heart is laid bare, and appears to depend entirely upon the sudden closure of the semilunar valves at the roots of the great arteries, this closure being effected by the column of blood pent up within the elastic parietes of these vessels; [the pressure from behind suddenly removed, the column immediately tends to return; but the semilunar valves are caught, smacked together, and the elastic force of the

its ventricular systole, it suddenly grasps, and becomes moulded upon, the unyielding charge of blood which it contains. From an elongated and triangular form, it is suddenly moulded into one that is nearly globular, and, resisted behind, it leaps forward and strikes the front wall of the chest. R. W.]

[870] Magendie, among others, held, that the first sound was owing to the stroke of the heart against the thoracic parietes. The notion is completely answered by the fact quoted above, viz. that the sound is still heard when there are no thoracic walls to strike against, [as it is also when the heart is removed from the body and is palpitating in the hand.] Carswell, [Rouanet, Bouillaud, and many others,] are of opinion, that the action of the mitral and tricuspid valves has a considerable or predominating influence in the production of the first as well as of the second sound of the heart. The conclusion of the committee of the British Association is, that this action is efficient only in a very minor degree in eliciting the first sound; which may gain something in definiteness of commencement perhaps through its influence, but nothing more.

arteries is then expended in urging on the blood in its proper course][871].

§ 400. The heart at each systole forces a certain quantity of blood, which has been estimated at about an ounce and a half, into the aorta, and the fluid at the same time flows per saltum through the arteries, the stroke of the heart being sensible as the pulse of these vessels even to very minute sub-divisions of their trunks[872]. However easy it is to appreciate the pulse of an artery, it is nevertheless extremely difficult to decide definitely on the state and relations of the vessel in connection with it. There seems little doubt but that in former times the contractility of arteries and its influence upon the circulation were overrated: in our own day, on the other hand, it is scarcely less certain that they have not been estimated at their full value; the latest experiments seem to prove that the arteries are not merely passively dilated with each stroke of the heart, and that they have a power over and above that which they

[871] The idea that the impinging of the wave of blood against the walls of the ventricles as it entered them from the auricles, must have a large amount of influence in engendering the first sound of the heart, as formerly maintained by Hope, is now little thought of; probably it is not without some influence; [but as the first sound is still distinct when the empty heart is contracting on the table, it cannot be very important.] The entire doctrine of the sounds and motions of the heart is evidently within the province of the Applied Physiology, and is very fully discussed in the many excellent works on Auscultation, which we now possess, amongst which may be mentioned, Barth and Rogers' *Manual*, and particularly the treatise of Skoda—*Abhandlung über Percussion, &c.* 2nd. ed. 1842.

[872] The left ventricle of the human heart will generally hold rather more than 1½oz, the right ventricle about 2oz. Some very small proportion of the blood must always be forced back at each systole. The doctrine of the circulation, and that of the pulse, so intimately connected with it, boast a very voluminous literature. Besides the works already quoted, I think it necessary to refer to the following particularly, Hale's *Statical Essays*, Lond., 1733. Poiseuille, *Rech. sur la force du cœur aortique*, in Magendie's *Journal*, vol. viii, p. 272, *Sur l'action des artères dans la circulation*, ib. vol. ix, p. 44. Parry, *An experimental enquiry into the nature, &c., of the Arterial pulse*, 1816. Hall, *A critical and experimental Essay on the Circulation of the Blood*, 1831. Wedemeyer, *On the Circulation—Untersuchungen über den Kreislauf des Blutes*, 1828, an excellent work, which besides many original inquiries, gives a very complete view of all that had been thought of and done on the subject. See also a supplement to the work, in Meckel's *Archiv*, 1828, p. 337. The article *Circulation*, in Todd's *Cyclopædia of Anatomy and Physiology*, by Dr. Allen Thomson, gives a brief and good view of the subject. Vide also, Burdach's *Physiology*, vol. iv.

possess in virtue of their simple elasticity[873]. The following general conclusions may be stated as the results of the vast number of experiments, which in recent times have been performed on the circulating system. 1*st*, THE ARTERIES POSSESS A NATURAL AND VERY CONSIDERABLE ELASTICITY, INDEPENDENT OF THEIR VITAL PROPERTIES, AND REMAINING IN GREAT FORCE EVEN AFTER DEATH. In virtue of this elasticity, the arteries maintain the forward motion of the blood begun by the systole of the heart; they contract upon and behind each new quantity of blood forced into them, accommodating themselves always to its amount, and thus keeping up a pressure at every point upon the mass, which as it is prevented from flowing back upon the heart by the closure of the semilunar valves, must needs advance in the course of the vessels. It is even easy to imitate or to produce a pulse in the dead body; it is only necessary to adapt a syringe to a large artery, and to force the piston down at regular short intervals. The middle elastic coat of the arteries plays the chief part in the act which has now been described. The vessels, as they are alternately distended and contracted, are of course constantly altering their diameters. The amount of contraction differs with the size of the artery; in small vessels it may be so considerable as entirely to obliterate their canals[874]. 2*d*, THE ARTERIES POSSESS A VITAL

[873] With these views of the particular influence of the vessels upon the advance of the blood, those that bear upon the mainsprings of the circulation in general are intimately associated, and will be fully discussed in the General Physiology. The views of different physiologists will be found stated in Wedemeyer, p. 69, et seq. That view according to which the heart is the sole source of the power which causes the blood to circulate, was maintained in former times by Harvey, Haller, and Spallanzani, and of late, by Jo. Müller and Magendie. The latter, in particular, has protested against any vital contractility of the arteries such as we have admitted in the text, and as was acknowledged by J. Hunter, Blumenbach, Söemmerring, Tiedemann. &c. Vide Magendie's *Leçons sur les Phenomènes physiques de la Vie*, vol. 2.

[874] This expansion and contraction of the calibre of arteries is easily observed, and measurements of its extent have been given by different observers. In a horse that was bled to death, Hunter found that the aorta contracted by $\frac{1}{10}$th, the iliac artery by $\frac{1}{6}$th, and the crural artery by $\frac{1}{3}$rd of their several original diameters. Arteries of the size of the radial, contracted to the entire obliteration of their cavites. Spallanzani observed the aorta of the newt enlarge by about $\frac{1}{3}$rd with each systole of the heart; he also perceived enlargements, but in a less degree, in the pulmonary artery, and in the main branches of the aorta. Accordant observations were made by Magendie, Poiseuille, Parry, Hastings, &c.

CONTRACTILITY DEPENDENT ON THE NERVOUS SYSTEM. Direct experiments have proved that the arteries contract and narrow their calibre on the application of chemical stimuli, of cold, perhaps also of galvanism, and that they aftewards relax, and regain their original diameter[875]. This contractility is principally resident in the annular fibrous layer of the middle coat, which in its intimate structure approximates to muscular tissue. The annular fibrous coat lies inwards from the longitudinal fibres, and forms the thickest layer in the walls of the great vessels. Undoubtedly upon this two-fold endowment of the arteries—simple passive elasticity, and organic contractility, depends their influence in the propulsion of the blood.

§ 401. From all that precedes it may be concluded that the pulse in the living body is an effect of the communication of an impulse from the heart to the column of blood contained in the arteries, in the course of which the artery suffers a slight displacement, and both its elasticity and vital contractility come into play. Without making these last admissions, it would be impossible to

See Schwann's Art. GEFAESSE in the *Berliner Encyclopæd. Worterb.*, for information on the great elasticity of the vessels.

[875] Irritability and active contractility cannot be refused the arteries in the face of recent experiments; the older doctrine, therefore, which accorded them both, again finds supporters. Vide Henle in Söemmering, p. 513. Schwann has mentioned one experiment which is easily repeated. Having the mesentery of a toad (Bufo igneus) under the microscope in the height of summer, when the weather was very warm, he found that an artery which measured 0,0724 of a line, after having had a few drops of cold spring water applied to it, contracted gradually in the course of from 10 to 15 minutes till it was 0,0276 of a line in diameter; by and by it began to dilate again, and in the course of about half an hour had regained its original diameter of 0,0724 of a line; the same phenomenon was observed repeatedly. Schwann extended his observations to the aorta and femoral artery of the frog, and found the phenomenon equally distinct; it was ever the more so as the animal had lost less blood previously. Schwann, l. c. p. 229. Thomson, Hastings, and Wedemeyer, produced contractions in arteries by the use of local stimuli, such as common salt, &c. Wedemeyer, on applying a galvanic stream from a battery consisting of from 14 to 20 pairs of plates, noted a distinct contraction in the arteries at the points galvanized, to the extent of $\frac{1}{4}$, $\frac{1}{2}$, and even $\frac{3}{4}$ths of the diameter of the cylinder, l. c. p. 242. Valentin's observations on the contraction of the aorta of the horse on irritation of the thoracic ganglia have already been noticed § 267. The capillary vessels have been repeatedly observed to contract under the influence of stimuli. Vide Henle, l. c. p. 513.

render any reason for the varieties of pulse, and various other phenomena, which are met with in pathological states[876]. The alternate dilatation and contraction of the arteries is partly active, partly passive. In virtue of their contractility, the arteries, like the muscles, appear to possess a continuous medium degree of contraction (tone). The rhythm of the pulse, however, is entirely a consequence of the stroke of the heart. The number of strokes of the pulse in any given time, coincides exactly with the number of contractions of the heart. The pulse is therefore more or less synchronous with the systole of the heart; it is only in arteries that are most remote from the heart that the arterial pulse is perceived to follow the stroke of the heart at a distinct interval, which may amount to about the $\frac{1}{6}$th of a second[877]. The number of beats is subject to the greatest individual and momentary varieties, and is also influenced by many different circumstances. It is influenced by age, sex, constitution, the time of the day, the season of the year, the state of repose or exertion, health or disease, etc., even the stature has an effect upon it. Whilst the pulse in the human fœtus varies from 140 to 150, and in the new-born infant is generally 130 in a minute, it sinks in age to 60, 50, and even a smaller number[878]. The simplest movements, such as changing the position, rising from the recumbent into the standing position, etc., increase the number of the pulse.

People of small stature have in general a more frequent pulse than men of larger bulk, and this influence of size seems to obtain very constantly among the lower animals. The larger the animal the slower in general is the pulse[879]. During pregnancy, in the

876 For example, the soft, the hard, the vibrating, and other kinds of pulse, the phenomena of inflammation, locally increased pulsations, &c.

877 Weber in particular found the pulse of the metatarsal artery upon the dorsum of the foot, to occur at from $\frac{1}{6}$th to $\frac{1}{7}$th of a second after the beat of the heart. *De Pulsu, &c.*, p. 2, Lips., 1834.

878 The number of the pulse at different ages may be stated as follows: in the first year at 120, in the second year at 110, in the third from 90 to 100, from the fourth to the fifteenth about 90, in youth 80, and in manhood from 70 to 75. It is impossible, however, to fix any kind of limits in this respect, as the greatest individual varieties are constantly met with. Irritable persons of a sanguine temperament have in general a much more frequent and variable pulse than phlegmatic persons.

879 In the adult horse and ox, the pulse is from 35 to 40, in the ass from 45

course of acute inflammatory diseases, of fevers, etc., the number of the pulse is more or less increased.

§ 402. The circulation in the veins is principally accomplished by the propulsive power of the heart. This influence of the heart upon the venous stream is readily demonstrated by making pressure upon the artery of a limb, when it will be seen that the veins which it feeds collapse or become distended, as the pressure upon the artery is increased or diminished. The veins, however, appear to possess active contractility, which cannot be without its influence upon the circulation[880]. The valves of the veins, and the pressure of neighbouring muscles and parts, also exert an influence upon the progress of the blood. There is no good foundation for the admission of any suction power of the heart, such as was formerly recognised, upon the great venous trunks that enter it[881].

to 50, in the sheep from 60 to 80, in the dog and cat from 90 to 100 per minute. See Gurlt's *Manual of Comparative Physiology*, p. 156.

880 Stimuli applied to the great venous trunks in particular have been observed to produce contractions, by Verschuir, Hastings, Bruns, Valentin, and others. See Henle, l. c. p. 517.

881 As facts proving this, we might quote with Wedemeyer, that the veins swell and become distended when they are tied, and farther the motion of the blood in the vena portæ, and in acardiac monsters. See Wedemeyer, l. c. p. 309. Parry in his *Experimental Researches on the Influence of Atmospherical Pressure upon the Blood in the Veins*, Lond. 1826, believed that he had observed in the course of his experiments, that coloured fluids only entered the jugular vein during the inspiration of the animals which were their subjects. From thence he infers, that the partial removal of the pressure of the atmosphere from the parts within the thorax during each inspiration, is the most efficient cause of the progression of the blood in the veins. Wedemeyer very properly observes by way of answer to this, that the fœtus has a very perfect circulation without any kind of respiratory movement. [One of the most powerful arguments for the influence of the inspiratory movement upon the progress of the blood, is afforded by the entrance of air into the veins in the course of surgical operations about the root of the neck. I know of no cause that can make the air rush with a hissing or guggling noise into the wounded jugular or subclavian vein, save the action of the thorax during inspiration. Beyond all question, however, the influence of the inspiratory movement can extend but a very short way along the great venous trunks, and in ordinary states it is probably altogether without effect on the progress of the blood,—the pulse is as full and regular during the longest expiration as it is during inspiration, and the circulation is perfect in animals which do not breathe by expanding and contracting a thoracic grating, as it is also in the fœtus, as observed by Wedemeyer. R. W.]

The rhythmical movement of the heart extends to the capillary arteries in a remitting, and to the veins at their commencements, in a continuous manner, when the motion of the blood becomes at the same time notably retarded[882].

Of Motion effected by Contractile Fibres which yield Gelatine.

§ 403. There are unquestionably contractile fibrous tissues in the human and animal body, concerning several of which we have already had occasion to speak, (as of the iris, § 316, of the arteries and veins, § 401 and 402), which, strictly considered, cannot be held to belong either to the purely muscular or cellular tissue. There are yet others of the same description, of which the dartos scroti may be taken as a type. This is a fibrous tissue, very similar to the general connecting or cellular tissue, but of a redder colour. The fibres combine into bundles, which compose a long-meshed network. It is by means of this tissue that the scrotum possesses the faculty of contracting into a hard ball, covered with transverse rugæ under the influence of cold. Internally the dartos passes into loose cellular tissue. It would appear from the latest inquiries, that the dartos is nothing more than modified cellular or common connecting tissue, more plentifully supplied with blood-vessels than usual. It would seem that the common integument acquired its tonic contractility, or faculty of contraction, from possessing an admixture of fibres of the same description as those that form the dartos. Probably, too, the longitudinal and annular fibres of the vascular system consist of a modified cellular tissue in the course of transition into muscular tissue; for not only do the trunks of the arteries and veins contract upon the application of stimuli, but that of the lymphatic system, or thoracic duct, does so likewise (§ 267). The majority of the contractile fibrous tissues are distinguished both chemically and histologically from the muscular tissue. The common cellular or connecting tissue may be assumed as the type of the histological form of these contractile fibrous tissues. Chemically considered, these tissues are distinguished from the muscular tissue

[882] This transition from a saltatory to a continuous motion is effected by the elasticity of the arteries. On this point, and others connected with it, see Weber, *De Pulsu, &c.*

by this, that they do not consist of fibrinc, and yield gelatinc by long boiling. The structurc, development, and vital endowments of these tissues, are still but imperfectly known; the consequence of which state of things is, that their limits and transitions cannot yet be precisely determined. It is probable that they will be found to form a progressive series, more and more highly organized as they advance from the simple connecting or cellular tissue, to the cross-streaked muscular fibre of animal life[883].

Of Ciliary Motions.

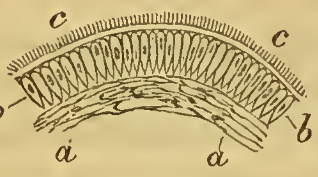
§ 404. The vibratile or ciliary motions constitute a peculiar class of motory phenomena. They appear to have been perceived by the older observers, but their cause, or the conditions on which they depend, were unknown; it is, indeed, only in very recent times that they have been studied in all their peculiarities, and that the great extent to which they take place has been discovered[884].

883 I have spoken of these tissues here, merely for the sake of connection and completeness. The works on general anatomy, particularly that of Henle, may be consulted for farther information in regard to their structure. The view at the conclusion of the above paragraph, appears to me to derive great support from the circumstance, that in one and the same system of organs we are frequently able to trace the transition and gradual completion of the contractile tissue; in the ciliary ligament and iris of birds, and in some lymphatic hearts, we find cross-streaked fibres, which are wanting in closely allied organs, or in the same organs of other animals. [The dartos of the human subject seems to have more than the mere tonic contractility alluded to in the text. The motions of the scrotum effected by its means appear to be definite, and even rhythmical, and consist of an alternate swaying from side to side, and of a kind of rotatory movement at the poles or points where the motions commence. R. W.]

884 Leeuwenhoeck, Swammerdam, and Ant. de Heide, were acquainted with the ciliary motion; the latter was probably the first who observed it—*Anatome Mytuli*, Amst. 1684. The proper discovery of its cause, however, and the development of the entire subject, belongs to Purkinje and Valentin: *De Phenomeno generali et fundamentali Motus Vibratorii continui in Membranis, &c., Com. Physiolog.*, Vratislav. 1835; and the *Supplement* published in the *Acta Acad. cæs. Natur. Curios.*, vol. xvii. p. 2. Dr. Sharpey gave an excellent account of the phenomena of ciliary motion based on personal observation pursued through the entire animal series, in the article Cilia, of the *Cyclopædia of Anatomy and Physiology*, 1836. [It ought to be stated, that Dr. Sharpey had been studying the subject of ciliary motions for some considerable time before

On very many parts, particularly the muco-membranous surfaces of the human and animal body, we observe, with the aid of the microscope, and only with its aid, numerous transparent filaments, leafets, or little hairs, (Fig. CCXXXVIII, *c, c*)[885], placed side by side in rows, and bearing a certain resemblance to the eye-lashes, whence the name CILIA, by which they are now generally known. The best of all subjects for studying these curious little bodies, are the avertebrata, and among them there are none better than the common fresh water mussel, (Anodonta,) and the members of the genus

Fig. CCXXXVIII.



Cyclas[886]. The cilia here, are about $\frac{1}{100}$th of a line in length, (*c, c*,) and are set upon rounded cells (*b, b*,) as upon bulbs; their motion is hook-like, that is to say, the point of each cilia successively approaches its base, and is suddenly stretched out again. In other cases, as in man and the mammalia, the cilia are frequently rather like leaves than hairs; but they still show the uncinate vibrations. Besides this kind of motion, another is noticed in many cases, which has been designated infundibuliform. Here the base is the centre around which the cilia sweep in a vortex or circle[887]. In

the appearance of Purkinje and Valentin's work; he had even made out the entire subject independently and for himself. His masterly paper referred to above will be read with great pleasure. R. W.]

[885] I take this opportunity of correcting a slight error in the representations of the cilia, which I have given in my *Icones Physiologicæ*. There ought to be no space betwixt the epithelial cylinders that support the cilia, and the cilia themselves; they are immediately sessile upon the epithelium, as in the plan figure, Fig. CCXXXIX, p. 696.

[886] A small piece of the edge of the mantle, or a portion of the gills of these animals, being placed upon a glass plate, having a drop of water added to it, and another thin plate of glass laid over it as a cover, will be found to exhibit the cilia and their motions to great advantage. The mucous membrane of the nose or fauces of the frog and rabbit, as also that of the trachea and Fallopian tube, may be selected as the best subjects for observing the phenomena of ciliary motion among vertebrate animals. The best way of proceeding is to snip off a little piece of the membrane with a pair of fine scissors, and to dispose it doubled or folded upon the port-object, so as to have the ciliary edge free for observation. The best attenuating medium here, is serum; and a power of from 300 to 500 linear is required for distinct vision.

[887] This infundibuliform motion, which Purkinje and Valentin mention, I

other instances still the cilia show a kind of vacillating or irregular motion, nodding as it were, and then standing erect[888]. When the cilia vibrate in rows, it is impossible during the period of highest activity of the motion, to distinguish the several cilia by which it is effected; all that is perceived is a glistering, particularly about the edge of the piece of membrane that is lying upon the port-object, as if a light were flickering, or a fluid were passing rapidly over its surface. After a time, or by making slight pressure upon the glass-plate which is used to cover the object, the cilia come out individually and more distinctly, and some of them are seen to vibrate more slowly. Now and then small detached portions of the object examined are observed that have no more than one, two, or three cilia, and these sometimes pass across the field propelled by the action of the vibratile bodies, as a boat is by its oars. Small particles of colouring matter, blood-discs, etc., added to the fluid, are perceived to be attracted towards, and then pushed suddenly away from the cilia, which are thus perceived to be possessed of the power to remove bodies or masses of matter relatively of very considerable magnitude[889].

Ciliary motions are observed very extensively in the animal kingdom. In the lowest forms of animal existence that people the sea,—polypes, echinoderms, medusæ, and molluscs—ciliary motions are noted on almost every free surface, upon the external integument, as well as upon the internal cavities; on the other hand, again, there are entire classes of animals, insects, for instance, in which the remarkable phenomenon of ciliary motion has not yet been observed. Among the vertebrata, its occurrence is somewhat limited, and it is observed most extensively, and of greatest intensity, in the amphibia. In the warm-blooded vertebrata and man, it ceases soon after death, although it is occasionally seen going on several hours after respiration has ceased; in the amphibia, how-

have not myself observed, any more than various other kinds of ciliary motion described by different other observers.

[888] The *motus vacillans* is esteemed the most frequent by Müller. It seems, however, rather to take place as a consequence of lessening power, and in spots; the primary movement is probably always of the kind which has been characterized as the *motus uncinatus*.

[889] I would refer here, to the ciliary motions of the inner aspects of arteries, § 110, and of the female genital organs, § 27 and 34.

ever, it not only continues for hours, but almost for days. The size of the cilia varies much in different cases, and may be stated at from $\frac{1}{500}$th to $\frac{1}{1000}$th of a line; in some cases they are so fine that they may be said to stand upon the confines of vision when aided by the best and most powerful microscopes[890].

§ 405. The remarkable feature in the ciliary motion, is its independence of the nervous system, of the integrity of the organ, and it might even be said, in a certain sense, of the organism itself. In the fresh-water mussel, the liveliest ciliary motions are often perceived going on for days, and almost weeks, upon the surface of detached portions of the animal; even when the animal, or portions of it, are far gone in putrefaction, the motions are still perceived very distinctly. In portions of the mucous membranes of decapitated tortoises, the same thing is perceived after several weeks have elapsed. In birds, all ciliary movement is generally at an end very speedily after death—after the lapse of a quarter of an hour or half an hour nothing more of it is to be perceived. In mammals, it generally continues for a few hours,—speaking generally, until the body has become cold; it consequently continues longer in warm than in cold weather. In the human subject, the phenomenon may be observed for hours upon portions of the mucous membrane of the nose, and of nasal polypi[891]. It is influenced variously by various reagents and circumstances. Some increase, others diminish or destroy it. Slight pressure, succussion, merely shaking the table upon which the microscope stands, suffice to increase the activity of the ciliary motions, and to arouse them anew when they have been flagging, or come to a stand still. Light does not seem to have any influence on them; no more have electricity and galvanism, unless, indeed, they are of such intensity as to decompose the animal tissues, when they act locally, and in a purely chemical manner: the cilia that are attained are destroyed, those that are not reached vibrate on. It is very remarkable that the substances which affect the nervous system so powerfully, such as hydrocyanic acid (diluted),

[890] For various other points of interest in connection with cilia, and ciliary motions, I must refer to Purkinje and Valentin's work, and to Dr. Sharpey's article CILIA.

[891] I have seen the ciliary motion continue for six hours on the surface of a nasal polypus, which had been extirpated.

morphine, strychnine, etc., have not the slightest influence on the cilia and their movements. It would seem that it is only when chemical substances are used of such strength as to destroy the animal tissues, that they have any effect on the cilia—the mineral acids, acetic acid, the caustic alkalis, corrosive sublimate, etc., put an end to the ciliary movement by destroying the cilia; saline matters, quinine, alcohol, etc., act less powerfully. Common, or distilled water, though it does not arrest, yet it retards the ciliary movement; tepid water gradually lessens its intensity.

The influence of the animal fluids upon the ciliary motion is very peculiar. Blood stimulates and sustains the action in the most remarkable manner. Portions of mucous membrane removed from the bodies of animals, and laid in whipped blood, will exhibit ciliary motions at the end of three days; whilst similar pieces placed in water will have lost their vibratile powers after the lapse of as many hours. From certain observations it appears, however, that the blood of the vertebrata only possesses a vivifying or enlivening power upon the ciliary movements of vertebrata; applied to parts of invertebrate animals which exhibit ciliary movements, the blood of vertebrate animals acts as a poison, immediately arresting all motion. Other organic fluids exert a vivifying or enlivening influence upon the ciliary phenomenon, and in the following order: milk, albumen, yolk of egg, urine,—the first having the greatest influence, the others less and less in their order. Bile tends to arrest the ciliary motion, both of vertebrate and invertebrate animals. The ciliary motions have been found quite normal in hybernating animals killed during the period of their unconsciousness[892].

§ 406. Up to this time ciliary motions have been observed in man, and the mammalia, in the following situations: the mucous membrane of the nasal passages, of the lachrymal duct, the palpebral conjunctiva, the upper part of the pharynx, the Eustachian tube, the greater part of the larynx and along the trachea and bronchi to their extremities, the female organs from the middle of the cervix uteri, through the tubes to the edges of the fimbræ; finally, the surface of all the cavities of the brain[893].

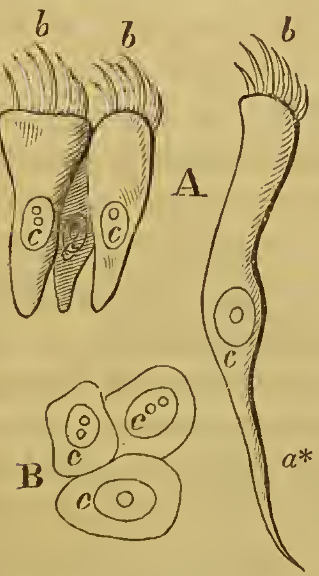
[892] The work of Purkinje and Valentin may be referred to as containing ample information upon all the topics which have been glanced at in the preceding paragraph.

[893] Vide Henle, (l. c. p. 245,) whose observations, in the main, I can confirm,

Wherever ciliary motions have been detected, cilia are seen as their instruments, set upon a particular form of epithelium,—the cylinder-epithelium, as it has been called, composed of closely set and generally conical cells, implanted perpendicularly upon the subjacent tissues. (Fig. CCXXXIX). Each cell supports several cilia upon its free summit, and internally contains a distinct nucleated nucleus. The cells of the ciliated epithelium vary somewhat in size and form in different parts[894]. Both the cells and the cilia are most delicate in the brain[895]. Each cylinder supports six, eight, or more cilia, which are sometimes of equal, sometimes of dissimilar length. The cilia, like the cylinders that support them, are deciduous formations, which are thrown off normally as well as in morbid conditions of the system; they appear in great numbers in the periodical discharge of the female, in catarrhs, etc.; although I hold it problematical that the cilia can be followed into the terminal vesicles of the bronchi.

[894] Some of the cylindrate epithelial cells are produced inferiorly into a point, *a** in the accompanying diagram, in which case the nucleus *c*, occurs about the middle of the formation. B, Is a transverse section of three ciliated cells to show the position of the nuclei and nucleoli. To obtain a view of the ciliary motion in man, we have but to draw the extremity of the handle of the scalpel over the mucous membrane of the nose, and to transfer the mucus that is thus obtained, properly prepared, to the stage of the microscope; it rarely happens that one or more epithelial cylinders with active cilia are not discovered. The tessular epithelium of the mucous membrane of the mouth may be procured by lightly scraping the inner surface of the cheek, and examined at the same time, by way of contrast.

Fig. CCXXXIX.



[895] Henle found cilia of great delicacy on the palpebral epithelium of the human subject. Analogy would incline us to believe that the minute yolk of the human ovum had the faculty of revolving on itself during its passage through the Fallopian tube, in consequence of possessing a delicate though transitory ciliary system. Bischoff, at least, has shown that this remarkable faculty is possessed by the yolk of the mammiferous animal's ovum. Müller's *Archiv*, 1841.

they are, however, very readily and rapidly reproduced[896]. Their functional significance is obscure[897]; nothing certain upon the subject is known, neither has the cause or mechanism of their motions been divined[898].

Of certain isolated Motory Phenomena.

§ 407. Certain motions are observed in the fine elementary parts, both of vegetables and animals, which, when carefully investigated, will be discovered to form steps of transition to the ciliary motions, and may prove the means of illustrating their nature. The motions alluded to are those that take place in isolated cells, and which, on this account, remind us of the isolated activity of the groups of cilia connected with the several cylinder-epithelial cells. In the polypes, actineæ, and medusæ, we meet with certain isolated superficial thin-walled vesicles,—microscopical capsules or cells,—which contain a number of delicate spiral filaments that can be projected, and that perform remarkable serpentine movements, bearing a remote resemblance to those of the spermatozoa[899]. The pigmentary cells or chromatophora of the cuttle-fish, are still more remarkable objects, their walls being elastic and contractile, and susceptible of

[896] Vide § 27.

[897] The influence of the ciliary action in aiding the access of the spermatic fluid to the ovum in the tube or ovary, has been already mentioned. That the cilia have a certain functional importance in the business of generation, is proclaimed by the fact of their existence beyond the vagina, and their appearance only with the period of sexual maturity. Vide § 39. It is quite obvious, farther, that they must be instrumental in brushing particles of mucus along the surface of the respiratory passages, of the Eustachian tube, &c., till they come within reach of the effort that is made in hawking or coughing, to be finally rejected.

[898] A certain appearance of streaking in the interior of ciliated cells, has been indistinctly perceived, and the conclusion jumped to, that this was evidence of the existence of delicate contractile fibres there, by which the motion was effected. With the optical instruments we possess at the present time, it is, however, impossible to come to any decision upon this point.

[899] I was formerly led erroneously to describe these formations in the actineæ as spermatozoa, vide § 6. Kölliker was the first to note their true nature: *Contributions, &c.—Beiträge zur Kenntniss der Geshlechtsverhältnisse, &c. wirbelloser Thiere*, Berl. 1841. I believe the parts which I have described as the stinging organ of the medusæ to be of the same kind: *Archiv für Naturgeschichte*, 1841, and *Icones Zootom.* Tab. 33 & 34.

being opened and shut like pulsating hearts. They often resemble stellate or ramified pigmentary cells, such as are found in the skin of the frog; or they are like the cells of the bone-corpuscles, and include nucleated nuclei in their interior[900]. They are the cause of the remarkable changes of colour presented by the animal.

To these motions of the cell-walls of the chromatophora of the cuttle-fish, we may, probably, assimilate those contractions and expansions of the yolk-cells of the planaria, those peristaltic and antiperistaltic motions by which the contents of each yolk-ball are incessantly forced hither and thither[901]. Here, too, we are reminded of the motions of the spermatozoa, which have already been particularly considered, those generally filamentary formations which at one period constitute the contents of cells, and of which the motions, still included in their parent cells, are often conspicuous[902]. Advancing still farther, we call to mind the motions of the otoliths within the sacculus of the cochlea, of which we have already spoken (§ 292)[903]. And here we come to the point at which we immediately pass to the motions that take place among the sap-globules within the cells of vegetables, and which we have an opportunity of observing so well in the Chara, Vallisneria, and other water plants; motions to which all the varieties that take place in plants,—those of the Oscillatoriæ, of the globules in the Closteriæ, and other low forms of vegetation—may be referred. These motions seem to lead us to the mysterious chemical agencies of the several cells, which we can only contemplate more particularly in the

900 See my paper just referred to in *Arch. f. Naturg.* S. 35, and *Icon. Zootom.* Tab. 29. The changes of colour observed in different other animals, such as the chameleon, are probably connected with some structure of the same description.

901 V. Siebold has observed these remarkable facts in the planaria, and made them the subject of a communication to the Royal Academy of Sciences of Berlin.—Vide the *Monatsbericht*, or Monthly Account of Proceedings of the Academy for February 1841.

902 Since my account of the motions of the Spermatozoa in the First Book was published, additional observations have been made by more than one physiologist, particularly by Kölliker, *Op. Cit.* Vide also my paper *On Pelagia Noctiluca*, and my *Icones Zootomicæ*, Tab. 33.

903 My latest observations incline me to refer the motions of the otoliths in the snail to ciliary actions. I believe that with a very fine instrument and careful illumination, I have distinctly seen the very delicate cilia by which the motions are accomplished.

General Physiology. It is indubitable, that in this direction there lies a rich field for observation still unexplored; and it seems likely, that starting from this point, we may find the means of answering many of the difficult questions which are constantly presenting themselves to the mind when somewhat close views are taken of the human and animal organisms [904].

[904] In connection with many of these tissues, I beg to refer to elementary works on Vegetable Physiology, to the General Physiology, and to a larger work which I have begun upon Organic Motory Phenomena in particular, and which will appear by and by. Many of the motions of vegetables are most intimately connected with their growth. [In connection with many of the vital motions and phenomena, I beg to refer particularly to a remarkable work upon *Caloric, in its Physical, Chemical, and Vital agencies*, by Samuel Metcalfe, M.D., which has just appeared. R. W.]

[APPENDIX.

Through the kindness of Dr Boyd, the resident medical officer of the Mary-le-bone Infirmary—an institution, which the zeal and intelligence of its Physicians and Surgeons has made to contribute so largely and so effectively to Medical Science, I am enabled to add a Table of the weight of the brain at different ages, from a large number of subjects, in confirmation of what is said in Annot. 763. This summary I cannot but think interesting, and calculated to settle the question in regard to the period at which the brain attains maturity in point of size. It is to be hoped that henceforth no one will be guilty of the folly of maintaining that a child of eight years of age has as large a brain as a full grown individual. I do myself the pleasure of adding Dr. Boyd's observations upon the Table.

"The small number of observations at the period from 10 to 20 years, and the accident of the female brains examined at that age being unusually large, may perhaps account for the average weight being greater than at either of the following periods, as there appears to be a tendency to increase till from 30 to 40 years, at which period, in the male, the brain arrived at its maximum, and also in the mean of both. From 40 to 50 years it decreased.

"This nearly corresponds with the late Dr. Sims' opinion, from 253 observations on the weight of the brain, to be found in vol. xix, *Medic. Chir. Transactions*.

"The difference between the weight of the male and female brain at each period of life is remarkable.

TABLE—*Showing the mean weight of the Human Brain, in ounces avoirdupois; the number of observations in each age of eight periods of life, in 349 Males, and 309 Females.*

AGES.	Number of Brains weighed.		Average weight.		Mean of both.	Total number of observations
	Male.	Female.	Male.	Female.		
2 to 5 years	32	25	38.519	36.085	37.416	57
5 to 10 —	17	20	41.691	39.956	40.753	37
10 to 20 —	18	16	45.138	43.89	44.551	34
20 to 30 —	40	44	46.178	43.306	44.672	84
30 to 40 —	68	52	47.689	43.62	45.926	120
40 to 50 —	82	74	47.108	42.422	44.883	156
50 to 60 —	72	63	46.868	42.991	44.243	135
60 & upwards	20	15	46.137	41.03	43.95	35

R. W.]

Marylebone Infirmary,
Dec. 11th, 1843.